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(NATURAL HISTORY)
11 JUN 1986
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Bulletin of the British Museum (Natural History)

Zoology series Vol 48 1985

British Museum (Natural History)
London 1985

Dates of publication of the parts

No 1	28 February 1985
No 2	25 April 1985
No 3	30 May 1985
No 4	31 October 1985

ISSN 0007–1498

Printed in Great Britain by Henry Ling Ltd, at the Dorset Press, Dorchester, Dorset

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Bulletin of the British Museum (Natural History)

Miscellanea

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The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

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Cromwell Road,
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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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The Zoology Series is edited in the Museum's Department of Zoology

Keeper of Zoology : Dr J. G. Sheals
Editor of Bulletin : Dr C. R. Curds
Assistant Editor : Mr C. G. Ogden

ISBN 0 565 05011 7
ISSN 0007-1498

Zoology series
Vol **48** No. 1 pp 1–74

British Museum (Natural History)
Cromwell Road
London SW7 5BD

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Indian Ocean echinoderms collected during the *Sindbad Voyage* (1980–81): 1. Holothurioidea

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Introduction

As a result of studies initiated during the last century (Semper, 1868; Ludwig, 1875, 1882, 1891; Bell, 1884–89; Théel, 1886; Pearson, 1913, 1914), and which have continued to the present time (e.g. Daniel & Halder, 1974; Sloan *et al.*, 1979; Aziz, 1981), knowledge of the systematics and distribution of Indian Ocean holothurians is appreciable. Many of the works are cited in the bibliographies of Domantay (1957), Clark & Rowe (1971), Jones (1971), Daniel & Halder (1974) and Rowe & Doty (1977). However, in spite of these surveys, information on holothurians in some parts of the Indian Ocean is still rather limited. These areas include certain remote island groups such as the Laccadives (Lakshadweep), as well as much of the area comprising Indonesia and Malaysia. With regard to the Laccadives, there is occasional mention of holothurians in the literature (e.g. Koehler & Vaney, 1908; Hornell, 1917; James, 1976), whereas apart from the 'Valdivia' Expedition (Heding, 1940) Sumatra appears not to have been included in any of the studies on Indonesian holothurians (e.g. Roberts, 1979; Roberts & Darsono, 1984; Aziz, 1981).

This paper represents an attempt to fill in some of the gaps in knowledge. Collections of holothurians (and other echinoderms) were made at the Laccadives, Sumatra and other localities during a voyage across the Indian Ocean from Oman to China. The expedition, *Sindbad Voyage*, was undertaken in 1980–81 using a replica of an ancient Arab sailing vessel, *Sohar*. For each of the 32 holothurian species collected, brief systematic notes are given, along with basic locality and habitat/depth information. Accounts of the other echinoderm classes/subclasses, and a detailed ecological study carried out in Sumatra, are to be published subsequently.

Methods

Specimens were collected by one of us (A.R.G.P.) and other expedition members at localities around Muscat, Oman; Chetlat Is., Laccadives; Beypore, India; Pula Wé Is., Sumatra. Details of the sampling areas are shown in Fig. 1. Sampling was undertaken principally on coral reefs using scuba. At each locality, details of habitat type and water depth, or depth range if exact depth was not noted, were recorded, along with the number of individuals of each holothurian species.

Material was relaxed, fixed and preserved using standard methods (Lincoln & Sheals, 1979). Some preliminary identifications were made by A.R.G.P. in the field and aboard *Sohar*, but the majority of specimens were identified by C.E.R. and checked by Miss A. M. Clark at the British Museum (Natural History), where the collections have been deposited.

Systematic account

Throughout this account, references are often given just to major works such as Clark & Rowe (1971) and Rowe & Doty (1977) from which the original specific descriptions can be traced.

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Bull. Br. Mus. nat. Hist. (Zool.) **48**(1): 1–9

Issued 28 February 1985

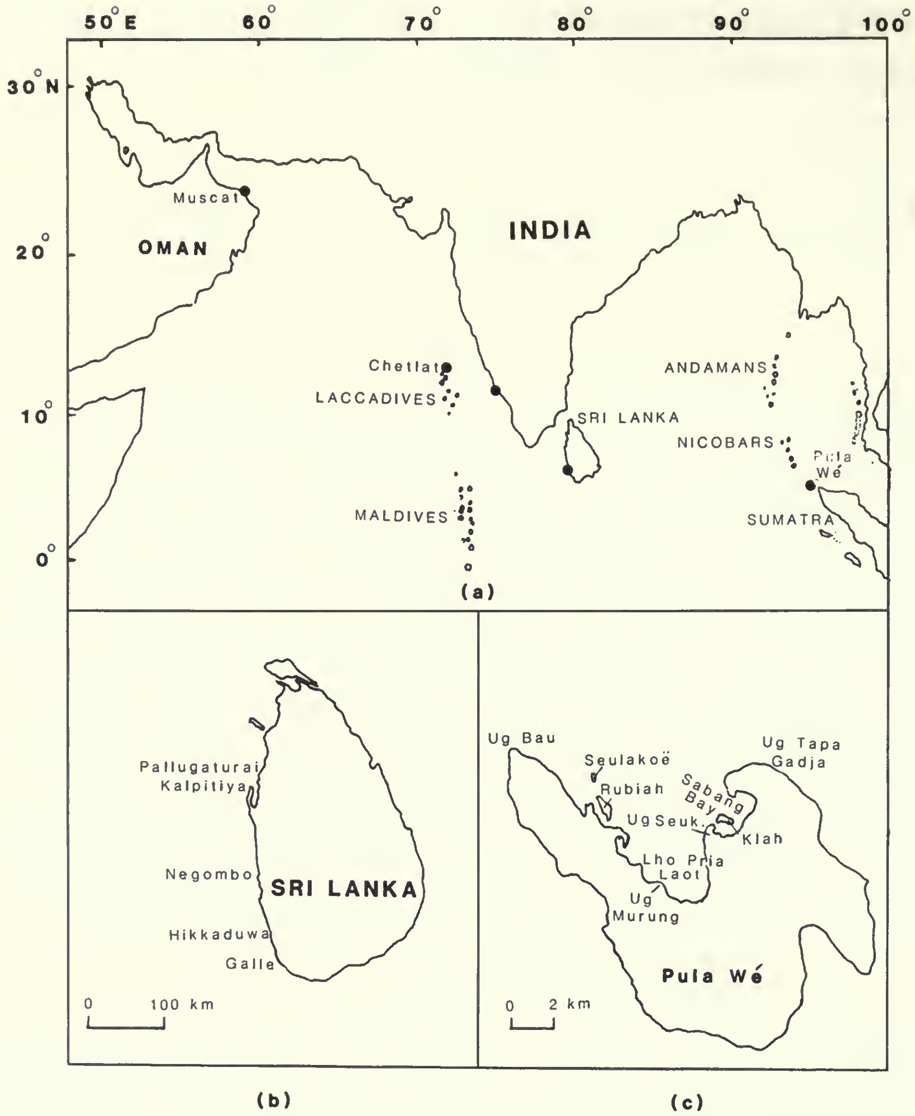

50°E
60°
70°
80°
90°
100°
30°N
20°
10°
0°
Muscat
OMAN
INDIA
Chetlat
LACCADIVES
ANDAMANS
SRI LANKA
NICOBARS
Pula Wé
MALDIVES
SUMATRA
(a)
Pallugaturai
Kalpitiya
Negombo
SRI LANKA
Hikkaduwa
Galle
0 100 km
Ug Bau
Seulakoë
Rubiah
Sabang Bay
Ug Seuk
Klah
Ug Tapa Gadja
Lho Pria Laot
Ug Murung
Pula Wé
0 2 km
(b)
(c)

Fig. 1 (a) Map of northern Indian Ocean showing sampling areas (●) during *Sindbad Voyage*, with insets for two areas sampled at several localities; (b) Sri Lanka; (c) Pula Wé, Sumatra.

References dealing with the biology of a species are sometimes also included, if the additional information is considered to be useful. This follows the practice of Sloan *et al.* (1979), and obviates the need for providing detailed synonymies.

Class HOLOTHURIOIDEA

HOLOTHURIIDAE

1. *Actinopyga echinites* (Jaeger, 1833)

See: Cherbonnier, 1955 : 136; Rowe & Doty, 1977 : 288.

Collection site: Galle, Sri Lanka (1 specimen).

Habitat & depth: Sublittoral bedrock; 5–10 m.

2. *Actinopyga lecanora* (Jaeger, 1833)

SEE: Koehler & Vaney, 1908 : 21 (as *Mülleria lecanora*); Clark & Rowe, 1971 : pl. 27, fig. 2.

COLLECTION SITES: Seulakoë, Ug Murung, SW Rubiah Is. and Ug Seukundo, Pula Wé, Sumatra (4 specimens & at least 5 observed but not collected).

HABITAT & DEPTH: Sublittoral rock, coral/sublittoral rock, coral reef sand; 2–20 m.

3. *Actinopyga mauritiana* (Quoy & Gaimard, 1833)

SEE: Rowe and Doty, 1977 : 228.

COLLECTION SITES: Chetlat Is., Laccadives: Hikkaduwa, Sri Lanka (2 specimens).

HABITAT & DEPTH: Coral reef, coral rubble; 2 m & 6 m.

4. *Actinopyga miliaris* (Quoy & Gaimard, 1833)

SEE: Panning, 1944 : 47 (as *A. lecanora miliaris*).

COLLECTION SITE: Klah, Pula Wé, Sumatra (1 specimen).

HABITAT & DEPTH: Coral reef sand; 4–5 m.

Actinopyga sp.

Individuals with details of spicules insufficiently distinctive for specific determination.

COLLECTION SITES: Muscat, Oman; Klah and Ug Bau, Pula Wé, Sumatra (3 specimens).

HABITAT & DEPTH: Coral reef sand; 2–20 m.

5. *Bohadschia graeffei* (Semper, 1868)

SEE: Rowe & Doty, 1977 : 229.

COLLECTION SITES: Chetlat Is., Laccadives; Ug Seukundo and Klah, Pula Wé, Sumatra (4 specimens).

HABITAT & DEPTH: Coral reef, coral reef sand; 4–20 m.

6. *Bohadschia marmorata* Jaeger, 1833

SEE: Rowe & Doty, 1977 : 229.

Collection sites: Chetlat Is., Laccadives; Ug Seukundo and Lho Pria Laot, Pula Wé, Sumatra (3 specimens).

HABITAT & DEPTH: Coral reef sand, sublittoral sand; 1–20 m.

7. *Labidodemas* sp.

Individuals with spicules insufficiently distinctive for specific determination.

COLLECTION SITE: SE Klah, Pula Wé, Sumatra (1 specimen).

HABITAT & DEPTH: Sublittoral rock; 2 m.

8. *Holothuria* (*Acanthotrapeza*) *coluber* Semper, 1868

SEE: Semper, 1868 : 90.

COLLECTION SITE: S Klah, Pula Wé, Sumatra (1 specimen).

HABITAT & DEPTH: ? Coral reef; 12–15 m.

9. *Holothuria* (*Acanthotrapeza*) *pyxis* Selenka, 1867

SEE: Rowe, 1969 : 138.

COLLECTION SITE: SE Klah, Pula Wé, Sumatra (1 specimen).

HABITAT & DEPTH: Sublittoral rock/coral; 2 m.

10. *Holothuria* (*Cystipus*) *rigida* (Selenka, 1867)

See: Rowe & Doty, 1977 : 234.

Collection site: SE Klah, Pula Wé, Sumatra (1 specimen).

Habitat & depth: Sublittoral rock/coral; 2 m.

11. *Holothuria* (*Halodeima*) *atra* Jaeger, 1833

See: Rowe & Doty, 1977 : 230; Bonham & Held, 1963 : 305 (ecology); Bakus, 1968 : 24 (ecology).

Collection sites: Muscat, Oman; Chetlat Is., Laccadives; Pallugaturai, Galle and SW Kalpitiya, Sri Lanka; N, S & SW Klah, SE Lho Pria Laot, E Sabang Bay and ?Ug Seukundo, Pula Wé, Sumatra (17 specimens). Individuals were also observed, but not collected, at several localities including Chetlat Is., where large numbers were present in a lagoon.

Habitat & depth: Intertidal mud/sand, mixed rock/coral and sand beach, sublittoral rock, coral rubble, coral conglomerate, coral sand; 0–15 m.

12. *Holothuria* (*Halodeima*) *edulis* Lesson, 1830

See: Rowe & Doty, 1977 : 231.

Collection sites: Muscat, Oman; SW Kalpitiya, Sri Lanka; Klah, Pula Wé, Sumatra (6 specimens). Individuals were also observed but not collected at other localities.

Habitat & depth: Sublittoral sand, often around coral or seagrass; 2–8 m.

13. *Holothuria* (*Lessonothuria*) *insignis* Ludwig, 1875

See: Ludwig, 1875 : 30.

Collection site: *c.* 3 km offshore from Negombo, Sri Lanka (1 specimen), representing new record for Sri Lanka area.

Habitat & depth: Coral reef; 5 m.

14. *Holothuria* (*Lessonothuria*) *pardalis* Selenka, 1867

See: Rowe & Doty, 1977 : 233.

Collection site: SE Klah, Pula Wé, Sumatra (1 specimen).

Habitat & depth: Sublittoral sand/rubble, sublittoral rock; 2 m.

15. *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835)

See: Rowe & Doty, 1977 : 233; Bonham & Held, 1963 : 305 (ecology).

Collection sites. Muscat, Oman; Galle, Sri Lanka (5 specimens).

Many other individuals were also observed (> 500 mm in length) but were not collected.

Habitat & depth: Mixed coral/rock and sand beach, sublittoral rock, coral reef; 0–5 m.

16. *Holothuria* (Microthele) *axiologa* H. L. Clark, 1921

See: Rowe & Doty, 1977 : 231.

Collection site; SW Klah, Pula Wé, Sumatra (1 specimen), representing new record for East Indies.

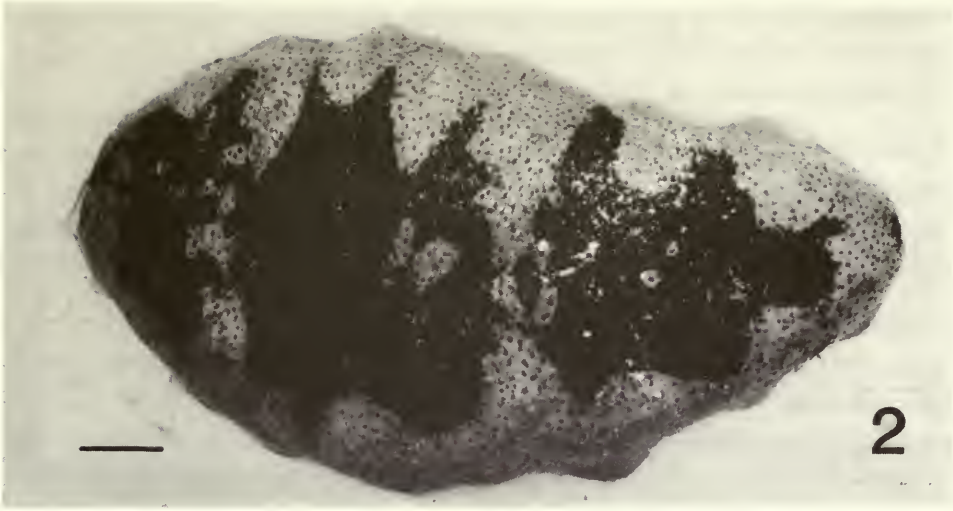
Habitat & depth: Coral reef sand; 4–5 m.

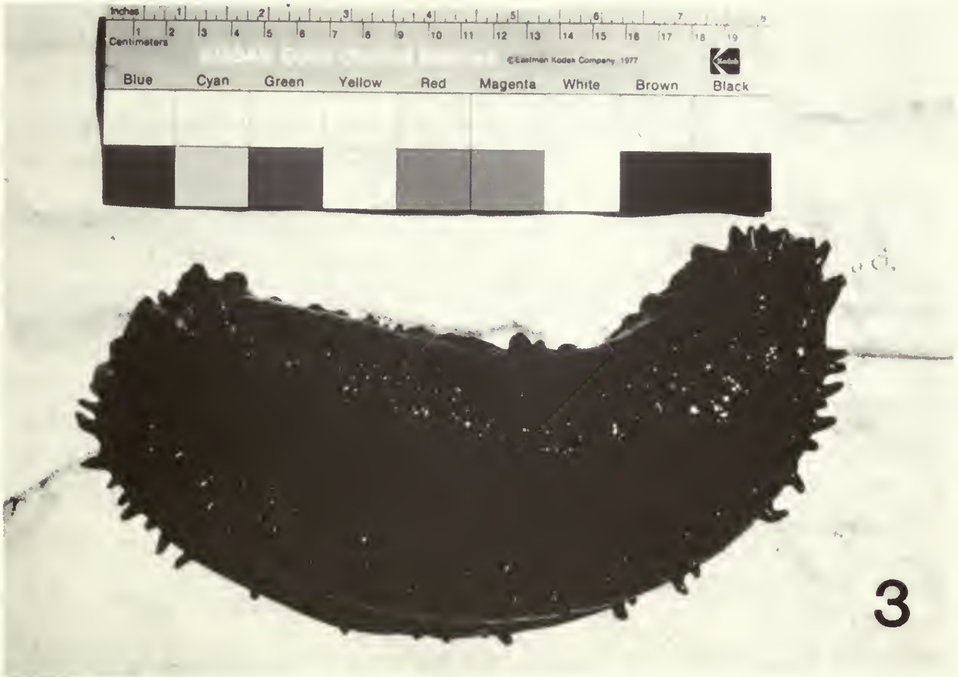
17. *Holothuria* (*Microthele*) *nobilis* (Selenka, 1867) . . . . Fig. 2

See: Rowe & Doty, 1977 : 231.

Collection sites: Chetlat Is., Laccadives: Ug Tapa Gadja, Pula Wé, Sumatra (2 specimens).

Habitat & depth: Coral reef sand, sublittoral sand; 0·5 & 10 m.

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Centimeters
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Yellow
Red
Magenta
White
Brown
Black
3

Fig. 2. *Holothuria* (*Microthele*) *nobilis* (Selenka) from Chetlat, Laccadives, (Scale = 2 cm).

Fig. 3 *Stichopus chloronotus* Brandt from Chetlat, Laccadives. (Scale indicated in photograph).

18. *Holothuria* (*Platyperona*) *difficilis* Semper, 1868

SEE: Rowe & Doty, 1977: 232; Bakus, 1968: 23 (ecology).

COLLECTION SITE: SW Kalpitiya, Sri Lanka (2 specimens).

HABITAT & DEPTH: Coral reef sand; 2 m.

19. *Holothuria* (*Selenkothuria*) *parva* Krauss *in* Lampert, 1885

SEE: Cherbonnier, 1952 : 503.

COLLECTION SITE: Nr Muscat, Oman (1 specimen).

HABITAT & DEPTH: Sand beach; 0 m.

20. *Holothuria* (*Semperothuria*) *flavomaculata* Semper, 1868

SEE Semper, 1868 : 87; Clark & Rowe, 1971 : pl. 27, fig. 15.

COLLECTION SITE: SW Kalpitiya, Sri Lanka (1 specimen), representing new record for Sri Lanka area.

HABITAT & DEPTH: Coral reef sand; 4 m.

21. *Holothuria* (*Semperothuria*) *imitans* Ludwig, 1875

SEE: Ludwig, 1875 : 33; Clark & Rowe, 1971 : pl. 27, fig 16.

COLLECTION SITE: Galle, Sri Lanka (1 specimen).

HABITAT & DEPTH: Coral reef; 4–5 m.

22. *Holothuria* (*Thymiosycia*) *hilla* Lesson, 1830

SEE: Rowe & Doty, 1977 : 232.

COLLECTION SITES: Muscat, Oman; Chetlat Is., Laccadives (3 specimens).

HABITAT & DEPTH: Coral reef sand, coral rubble; 0·5 & 2 m.

STICHOPODIDAE

23. *Stichopus chloronotus* Brandt, 1835 . . . . Fig. 3

SEE: Rowe & Doty, 1977 : 227.

COLLECTION SITES: Chetlat Is., Laccadives; SW Klah, N Rubiah Is., Pula Wé, Sumatra (4 specimens). Other individuals were also observed but not collected.

HABITAT & DEPTH: Coral reef sand, sublittoral rock/coral; 0·5–9 m.

24. *Stichopus horrens* Selenka, 1867

SEE: Rowe & Doty, 1977 : 227.

COLLECTION SITE: Klah, Pula Wé, Sumatra (1 specimen, partly decomposed).

HABITAT & DEPTH: Coral reef sand; 12–15 m.

25. *Stichopus variegatus* Semper, 1868

SEE: Sloan *et al.*, 1979 : 124.

COLLECTION SITES: Muscat, Oman; Ug Murung, Pula Wé, Sumatra (2 specimens). Individuals were also observed but not collected.

HABITAT & DEPTH: Coral reef, sublittoral rock; 3 m.

26. *Thelenota ananas* (Jaeger, 1833)

SEE: Rowe & Doty, 1977: 227.

COLLECTION SITES: N & SW Klah and SW Ug Bau, Pula Wé, Sumatra (3 specimens).

HABITAT & DEPTH: Coral reef sand, sublittoral rock; 4–22 m.

CUCUMARIIDAE

27. *Leptopentacta imbricata* (Semper, 1868)

SEE: Panning, 1966 : 57; Clark & Rowe, 1971 : pl. 29, fig. 5 (as *L. javanicus*).

Collection site: Beypore, India (5 specimens), representing new record for W India & Pakistan area.

Habitat & depth: Sublittoral mud; 9 m.

28. *Plesiocolochirus* sp.

Spicule configuration insufficiently distinctive for specific determination.

Collection site: Pallugaturai, Sri Lanka (5 specimens), representing new record of genus in Sri Lanka area. Many other individuals were also observed but not collected.

Habitat & depth: Intertidal mud and sand; 0 m.

SYNAPTIDAE

29. *Synapta maculata* (Chamisso & Eysenhardt, 1821)

See: Rowe & Doty, 1977 : 234.

Collection sites: Chetlat Is., Laccadives: SW Rubiah Is., Pula Wé, Sumatra (2 specimens, one of which was *c.* 2 m long when alive).

Habitat & depth: Coral reef sand; *c.* 2–10 m.

30. *Synaptula alba* Heding, 1928

See: Heding, 1928 : 171.

Collection sites: Ug Murung and S Ug Bau, Pula Wé, Sumatra (2 specimens, > 1 m in length when alive).

Habitat & depth: Sponge, sublittoral rock/rubble; 18–20 m.

31. *Synaptula reticulata* (Semper, 1868)

See: Semper, 1968 : 13 (*as Synapta reticulata*)

Collection site: Ug Bau, Pula Wé, Sumatra (20 specimens).

Habitat & depth: Sponge; 40 m.

Synaptula sp.

Spicule configuration insufficiently distinctive for specific determination.

Collection sites: S & SE Klah, Pula Wé, Sumatra (2 specimens).

Habitat & depth: Coral reef, sublittoral rock/rubble; 2–8 m & 10 m.

CHIRIDOTIDAE

32. *Chiridota stuhlmanni* Lampert, 1896

See: Heding, 1931 : 676.

Collection site: S Klah, Pula Wé, Sumatra (2 specimens), representing new record for East Indies.

Habitat & depth: Coral reef; 2–8 m.

Discussion

At least 32 species of holothurians are here reported as a result of collections made during the *Sindbad Voyage*. These are all shallow Indo-West Pacific species, often of widespread distribution and probably originating largely from the Indonesian area. Following the zoogeographic divisions of the Indo-Pacific adopted by Clark & Rowe (1971), one genus and 5 species are newly recorded: W India & Pakistan (1 species); Sri Lanka area (1 genus & 2 species) and the East Indies (2 species). Their previously known limits of range are indicated below.

Holothuria (*Lessonothuria*) *insignis*–Mascarene Is. and E Africa & Madagascar; Bay of Bengal eastwards to S Pacific Is.

Holothuria (*Microthele*) *axiologa*–N Australia and S Pacific Is.

Holothuria (*Semperothuria*) *flavomaculata*–Red Sea; E Indies, Philippine Is, and S Pacific Is.

Leptopentacta imbricata–SE Arabia, ?Maldive area, Sri Lanka area eastwards (excluding N Australia) to China & S Japan.

Plesiocolochirus–Three Indo-Pacific species are recognised, previously recorded only in the E Indies and N Australia.

Chiridota stuhlmanni–Is. of W Indian Ocean, E Africa & Madagascar and Red Sea; Sri Lanka area and S Pacific Is.

In most cases, the new holothurian records extend the range westwards from the eastern side of their known distribution. With the exception of *H.* (*M.*) *axiologa* and *Plesiocolochirus* sp., it can be seen that these holothurians also occur on the western side of the Indian Ocean.

Acknowledgements

We are grateful to Dr R. Dalley, P. Hunnam, P. Dobbs and D. Tattle for their considerable assistance during field work. One of us (A.R.G.P.) would also like to thank Tim Severin, leader of *Sindbad Voyage*, for the kind invitation to participate in the expedition which was made possible by generous sponsorship from the Ministry of National Heritage and Culture, Oman. Special thanks are due to Miss A. M. Clark, British Museum (Natural History) for checking identifications and making useful comments on the manuscript, and also to Dr F. W. E. Rowe for identifying one of the specimens.

References

Aziz, A. 1981. The echinoderms collected from the coral reefs of Pari Islands, Seribu Islands (in Indonesian). *Oseanologi di Indonesia* **14:** 41–50.

Bakus, G. J. 1968. Defensive mechanisms and ecology of some tropical holothurians. *Marine Biology Berlin* **2:** 23–32.

Bell, F. J. 1884. Echinodermata. *In:* Coppinger, R. W. *Report on the Zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. 'Alert', 1881–82.* Trustees of the British Museum, London. pp. 117–177 & 509–512.

—— 1885. On the echinoderm fauna of the island of Ceylon. *Report of the British Association for the Advancement of Science. London* **1885:** 1065.

—— 1886. On the holothurians of the Mergui Archipelago collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson. *Journal of the Linnean Society of London* (Zoology) **20:** 25–28.

—— 1887. Report on a collection of Echinodermata from the Andaman Islands. *Proceedings of the Zoological Society of London* **1887:** 531–534.

—— 1888*a*. Report on a collection of echinoderms made at Tuticorin, Madras, by Mr E. Thurston. *Proceedings of the Zoological Society of London* **118:** 383–389.

—— 1888*b*. On the Echinodermata of the Sea of Bengal. *Report of the British Association for the Advancement of Science* **1888:** 718.

—— 1889. Additions to the echinoderm fauna of the Bay of Bengal. *Proceedings of the Zoological Society of London* **1889:** 6–7.

Bonham, K. & Held, E. E. 1963. Ecological observations on the sea cucumbers *Holothuria atra* and *H. leucospilota* at Rongelap Atoll, Marshall Islands. *Pacific Science. Honolulu* **17:** 305–314.

Cherbonnier, G. 1952. Contribution á la connaissance des Holothuries de l'Afrique du Sud. *Transactions of the Royal Society of South Africa. Cape Town* **33:** 469–509.

—— 1955. Rèsultats scientifiques des campagnes de la 'Calypso'. Les holothuries de la Mer Rouge. *Annales de l'Institut Océanographique. Monaco & Paris* **30:** 129–183.

Clark, A. M. & Rowe, F. W. E. 1971. *Monograph of the Shallow-Water Indo-West Pacific Echinoderms.* 1–238 pp., London.

Daniel, A. & Halder, B. P. 1974. Holothuroidea of the Indian Ocean with remarks on their distribution. *Journal of the Marine Biological Association of India* **16:** 412–436.

Domantay, J. S. 1957. The zoogeographical distribution of the Indo-Pacific Holothurioidea. *Proceedings of the 8th Pacific Science Congress* **3:** 417–455.

Heding, S. G. 1928. Synaptidae. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* **85:** 105–323.

—— 1931. Uber die Synaptiden des Zoologischen Museums zu Hamburg. *Zoologischer Jahrbücher. Jena* (Systematik) **61:** 637–696.

—— 1940. Die Holothurien der deutschen Tiefsee-Expedition. 2. Aspidochirote und Elasipode Formen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf den dampfer 'Valdivia'.* **24:** 317–375.

Hornell, J. 1917. The Indian *beche-de-mer* industry, its history and recent revival. *Madras Fisheries Bulletin* **11:** 119–150.

James, D. B. 1976. The *beche-de-mer* resources of India. In: *The Proceedings of the Symposium on Living Resources of the Seas around India.* pp. 706–711.

Jones, S. (Ed.) 1971. *Bibliography of the Indian Ocean.* Marine Biological Association of India. 1–573 pp.

Koehler, R. & Vaney, C. 1908. Littoral Holothuroidea. *Echinoderma of the Indian Museum.* Calcutta. pp. 1–54.

Lincoln, R. J. & Sheals, J. G. 1979. *Invertebrate Animals: Collection & Preservation.* British Museum (Natural History) & Cambridge University Press. pp. 1–150.

Ludwig, H. 1875. Beiträge zur Kentniss der Holothurien. *Arbeiten aus dem Zoologisch-Zootomischen Institut in Würzburg* **2:** 77–120.

——1882. List of the Holothurians in the collection of the Leyden Museum. *Notes from the Leyden Museum. Leiden* **4:** 127–137.

—— 1891. Bemerkungen über einige ceylonesisches Echinodermen. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens. Bonn* **47:** 98–105.

Panning, A. 1944. Die Trepangfischerei. *Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg* **49:** 1–76.

—— 1966. Bemerkungen über die Holothurien-Familie Cucumariidae (Ordnung Dendrochirota). 5. Die Gattungen *Heterothyone* Panning, 1949 und *Leptopentacta* H. L. Clark, 1938. *Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg* **63:** 51–59.

Pearson, J. 1913, 1914. Notes on the Holothurioidea of the Indian Ocean. *Spolia Zeylanica* **9:** 49–101: 173–190.

Roberts, D. 1979. Deposit feeding mechanisms and resource partitioning in tropical holothurians. *Journal of Experimental Marine Biology and Ecology. Amsterdam* **37:** 43–56.

—— **& Darsono, P.** 1984. Zonation of reef flat echinoderm at Pari Island, Seribu Islands, Indonesia. *Oseanologi di Indonesia* No. 17: 33–41.

Rowe, F. W. E. 1969. A review of the family Holothuriidae (Holothurioidea Aspidochirodita). *Bulletin of the British Museum (Natural History).* London (Zoology) **18:** 119–170.

Rowe, F. W. E. & Doty, J. E. 1977. The shallow-water holothurians of Guam. *Micronesica* **13:** 217–250.

Semper, C. 1868. Holothurien. *Reisen in Archipel der Philippinen.* 2. Wissenschaftliche Resultate. 1–288 pp. Wiesbaden.

Sloan, N. A., Clark, A. M. & Taylor J. D. 1979. The echinoderms of Aldabra and their habitats. *Bulletin of the British Museum (Natural History). London* (Zoology) **37:** 81–128.

Théel, H. 1886. Holothurioidea. Part 2. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873–76. London* **39:** 1–290.

Manuscript accepted for publication 6 June 1984

A new genus of West African earthworm with notes on the identity of *Iridodrilus* Beddard, 1897 (Eudrilidae : Oligochaeta)

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In 1897 Beddard described an earthworm found in soil received from Lagos which because it had fewer intestinal gizzards, three, compared with species of his monotypic genera *Hyperiodrilus* and *Heliodrilus* from the same region each with six intestinal gizzards, he recognized as a new genus and species, *Iridodrilus roseus*. His action was acceptable since although few earthworms with intestinal gizzards were known at that time, among groups with oesophageal gizzards, the number and location were considered to be of primary taxonomic significance. Consequently in the Eudrilinae (Michaelsen, 1900), species with six intestinal gizzards came to be assigned to *Hyperiodrilus*, with *Heliodrilus* being reduced to a synonym by page priority, while species with three intestinal gizzards were accommodated by *Iridodrilus*, for example the otherwise dissimilar species from the Cameroons, *I. preussi* Michaelsen, 1903.

This simplistic solution obscured the true affinities of some of the included species and many years elapsed before further material was collected that led to a morphological re-examination and appraisal of affinities of the species. Evidence that the numbers of intestinal gizzards could vary within a genus came with the description of new species of *Legonea* by Sims (1964) and Clausen (1967), and of *Hyperiodrilus* by Sims (1965) and Clausen (1967). Next it was shown that the possession of the same number of intestinal gizzards did not necessarily constitute grounds for making two species congeneric. Series from the vicinity of Ibadan possessed six intestinal gizzards but were found to have a basically paired spermathecal system below, or alongside, the gut like that described in *Heliodrilus lagosensis* and unlike *Hyperiodrilus africanus* that has perioesophageal ducts uniting dorsally in a single supra-intestinal receptaculum seminis; thus *Heliodrilus* and *Hyperiodrilus* were separated (Sims, 1977). In my opinion a similar situation persists in the genus *Iridodrilus* caused by overemphasis of the criterion of the presence of three intestinal gizzards for the inclusion of a species in the genus. This practice has resulted in dissimilar taxa, the poorly described *roseus* Beddard and the well-defined *preussi* Michaelsen being placed together while more recently the situation has been further confused when a new species *I. vomiensis* was described together with a close ally *I. tonyii* that has four intestinal gizzards (Segun, 1977*a*). Accordingly to obtain more detailed information on the morphology of the type species of the genus than originally provided by Beddard, the two syntypes of *I. roseus* (BM(NH) 1904.10.5.962) were re-examined.

Part I

Iridodrilus roseus Beddard, 1897

Iridodrilus roseus Beddard, 1897. Proc. zool. Soc. Lond. **1897,** p. 346.

Description. *External characters*. Length 58, 76 mm, diameter 3 mm. Segments 94, 143; tending towards a biannulate condition. Dorsal pores absent. Clitellum almost annular but with a pale midventral stripe where the ventral edges fail to meet, thus strictly the clitellum should be regarded as being saddle-shaped. Male pore single, midventral in furrow 17/18, seen as a boss-like porophore with a longitudinal slit. Penial setae absent. Female pores paired ventrally near the equator of segment *xiv,* located setal distance 2*ab* within setal lines *aa*. Spermathecal pore single, midventral in furrow 12/13, carried on a low but broad porophore extending $\frac{1}{2}$*xii*–$\frac{1}{2}$*xiii*. Nephridiopores paired between setal lines *cd*.

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Setae eudriline, $ab > cd$; postclitellar setal formula $aa:ab:bc:cd = 9:6:5:1$ where dd is equal to half the body circumference.

Internal characters. Septa 4/5–12/13 thickened. Oesophageal gizzard(s) absent; three intestinal gizzards present *xviii, xix, xx*. Calciferous glands paired *xiii*, suboesophageal pouches well-developed *x* and *xi* (i.e. absent from *ix*). Holandric, each testis is enclosed in a testis sac formed from the ental end of the vas deferens and continuous with its seminal vesicle; the seminal vesicles appear to be convoluted but on unfolding are found to be simply digitiform. Euprostates are long and extend for several segments behind *xviii*. Spermathecal atrium muscular extendimg from the hind region of *xii* nearly to $\frac{1}{2}$*xiv*, the hinder region opens ventrally into a membranous subintestinal receptaculum seminis that posteriorly tapers to septum 16/17 and anteriorly gives off a pair of massive lateral pouches that flex back alongside the tapering medial portion. Each pouch is constricted posteriorly to form a slender convoluted duct that leads forwards to the fertilization chamber of its side. Ovaries paired on the fertilization chambers from which long oviducts lead into the ventral parietes by the vasa deferentia midsegmentally in *xiv*. A slender membranous duct, ? relict ovarian duct, leads forwards from each ovary to unite below the spermathecal atrium (Fig. 1). Excretory system holonephridial.

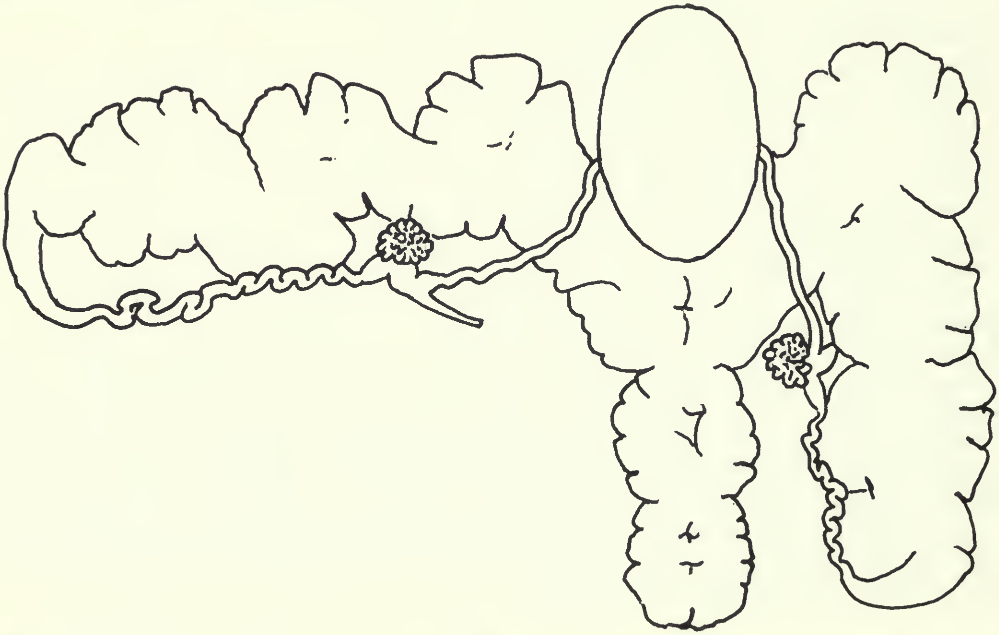

Fig. 1 *Iridodrilus roseus* syntype. Female and spermathecal systems, dorsal view with the left side displaced laterally.

Remarks. The spermathecal system of *Iridodrilus roseus* is similar to that present in *Heliodrilus lagosensis* Beddard, 1891 (Sims, 1977, Fig. 5). In both the pore is single but the system is basically paired with massive pouches that posteriorly give way to slender ducts communicating with the fertilization chambers. In *H. lagosensis* the medial portion of the receptaculum seminis is wanting also the lateral pouch of one side usually fails to develop but the basic pattern remains sufficiently similar to reveal the close affinity of the two species. It is especially interesting that in *roseus* a membranous coelomic duct joins the two fertilization chambers like the communicating duct in *lagosensis* and could become similarly functional to supply sperm to both fertilization chambers if one of the lateral pouches of *roseus* were to fail to develop. But the greatest similarity between *lagosensis* and *roseus* is found in the number and location of the suboesophageal pouches; in the specimens of *lagosensis* examined these pouches are reduced or absent from segment *ix* as in *roseus*. (Beddard, 1891:255, miscounted the segments and reported the presence of 'the first of the two oesophageal pouches' in *xi*, a second in *xii* then a vestigal third in *xiii* before listing the paired calciferous glands in *xiv*). In view of these similarities and the undoubted mutual affinities of the species, I believe that *lagosensis* and *roseus* are congeneric.

Genus ***HELIODRILUS*** Beddard, 1890

Heliodrilus Beddard, 1890. Zool. Anz. **13,** p. 627. Type by monotypy *Heliodrilus lagosensis* Beddard, 1891.

Iridodrius Beddard, 1897. Proc. zool. Soc. Lond. **1897,** p. 346. Type by monotypy *Iridodrilus roseus* Beddard, 1897.

DIAGNOSIS. Eudrilinae with setal distance *ab*>*cd*. Male pore single 17/18 and several segments anteriorly spermathecal pore single. Penial setae absent. Female pores paired *xiv* or 14/15. Oesophageal gizzard(s) absent, intestinal gizzards present; suboesophageal pouches single *x* and *xi*, calciferous glands paired *xiii*. Spermathecal system paired internally (although one side may fail to develop), paired pouches lead back from the spermathecal pore (or atrium), posteriorly each reduces to a slender duct that passes forwards to the fertilization chamber of its side: a coelomic duct joins the two fertilization chambers.

INCLUDED SPECIES. *lagosensis* Beddard, 1891; *roseus* (Beddard, 1897) ***comb. nov.***

DISTRIBUTION. Nigeria (Beddard, 1891: 253 & 1897: 364; Segun 1977a: 588 & 1978: 30; Sims, 1977: 537).

NOTE. The species can be readily distinguished by the presence of several unpaired papillae between *xi* and *xviii* on the ventral surface of *lagosensis* (papillae absent in *roseus*), internally only one pouch usually develops to form a single receptaculum seminis in *lagosensis* (spermathecal elements paired throughout in *roseus*), seminal vesicles digitiform in *roseus* (seminal vesicles unspecialized in *lagosensis*).

Part II

Although the species *roseus* Beddard is now placed in the genus *Heliodrilus*, other species previously associted with it differ in important details and cannot be similarly assigned. These species superficially resemble *roseus* by having only three or four intestinal gizzards but they differ in having paired rolled-tube penial setae and the paired calciferous glands in *xii*. The more anterior location of the calciferous glands seemingly links the species with the *Eudrilus* group of genera and in particular *Nsukkadrilus* which has additionally both rolled-tube penial setae and intestinal gizzards (Segun, 1977*b*) but they differ in the separation of the female and spermathecal pores. A new genus is accordingly proposed to accommodate the species.

Genus ***SEGUNIA*** gen. nov.

DIAGNOSIS. Eudrilinae with setal distance *ab*>*cd*. Male pore single 17/18 and several segments anteriorly spermathecal pore single. Paired rolled-tube penial setae present. Female pore paired laterally on *xiv*. Oesophageal gizzard(s) absent, intestinal gizzards present; suboesphageal pouches single *x* and *xi*, calciferous glands paired *xii*. Spermathecal system paired internally; paired pouches lead back from a medial atrium or receptaculum, posteriorly each reduces to a slender duct that passes forwards to the fertilization chamber of its side; a coelomic duct joins the two fertilization chambers.

TYPE. *Iridodrilus preussi* Michaelsen, 1902.

INCLUDED SPECIES. *preussi* (Michaelsen, 1902) **comb. nov.;** *tonyii* (Segun, 1977*a*) **comb. nov.;** *vomiensis* (Segun, 1977 *a*) **comb. nov.**

DISTRIBUTION. Cameroons (Michaelsen, 1902); Nigeria (Segun, 1977*a* & *b*; 1980).

NOTE. The species may be distinguished externally by differences in their papillae patterns (Segun, 1977*a*) and internally by the number and location of the intestinal gizzards: *preussi xviii, xix, xx; vomiensis xix, xx, xxi; tonyii xx, xxi, xxii, xxiii.*

The new genus is named in honour of Dr A. O. Segun, Museum of Natural History, University of Ife, Ile-Ife, Nigeria.

References

Beddard, F. E. 1890. Preliminary note upon *Heliodrilus,* a new genus of Eudrilidae. *Zoologischer Anzeiger* **13:** 627–629.

—— 1891. On the structure of two new genera of earthworms belonging to the Eudrilidae, and some remarks on *Nemertodrilus. Quarterly Journal of Microscopical Science* (New Series) **32:** 235–278.

—— 1897. On a collection of earthworms from South Africa belonging to the genus *Acanthodrilus. Proceedings of the Zoological Society of London* **1897:** 336–349.

Clausen, M. W. 1967. The African oligochaete genera *Hyperiodrilus* Beddard, 1891 and *Legonea* Clausen, 1963 (Oligochaeta). *Videnskabelige Meddeleser fra Dansk Naturhistorisk Forening i Kjøbenhavn* **130:** 179–207.

Michaelsen, W. 1900. Oligochaeta. *Das Tierreich* **10:** ii–xxix & 1–575.

—— 1902. Neue Oligochaeten und neue Fundorte alt-bekanntern. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* **19:** 1–54.

Segun, A. O. 1977*a*. The genus *Iridodrilus* (Eudrilidae: Oligochaeta) in Nigeria. *Journal of Natural History* **11:** 579–589.

—— 1977*b*. Eudrilin earthworms, including a new genus, from eastern Nigeria. *Proceedings of the Biological Society of Washington* **90** (2): 255–262.

—— 1978. Eudrilid earthworms from Ile-Ife, western Nigeria. *Journal of Natural History* **12:** 15–31.

—— 1980. More eudriline earthworms from eastern Nigeria. *Journal of Natural History* **14:** 271–281.

Sims, R. W. 1964. Internal fertilization and the functional relationship of the female and spermathecal systems in new earthworms from Ghana. *Proceedings of the Zoological Society of London* **143:** 587–608.

—— 1965. Acanthodrilidae and Eudrilidae (Oligochaeta) from Ghana. *Bulletin of the British Museum (Natural History)* (Zoology) **12:** 283–311.

—— 1971. Eudrilinae from southern Nigeria and a taximetric appraisal of the family Eudrilidae (Oligochaeta). *Journal of Zoology, London* **164:** 529–549.

Manuscript accepted for publication 9 July 1984

Mites of the genus *Calcarmyobia* (Acarina, Myobiidae) with information on the taxonomy of their host bats of the genus *Miniopterus* (Chiroptera, Miniopteridae)*

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Introduction

The tendency to regard the genus *Calcarmyobia* Radford as monotypic was prevalent until the beginning of the 1970s. The eight known species of the genus have been described on strict definition of each species (Uchikawa, 1982), and it is gradually proved that the mites of the genus *Calcarmyobia* are specific parasites of bats of the genus *Miniopterus*. Referring to the present knowledge of the mites, such formerly proposed specific names *Calcarmyobia miniopteris* and *C. parenzani* for species from South Africa and Europe, respectively, as well as some host records, should be revised (Uchikawa, 1984).

Mites of the genus *Calcarmyobia* have been evaluated as good indicators in the taxonomy and phylogeny of their host bats (Uchikawa & Harada, 1981). As the taxonomy of *Miniopterus* is not in a satisfactory state, an accumulation of records of the mites is believed to give a clue for solving some complicated problems in this area.

The present author had an opportunity to examine for ectoparasites the bat specimens deposited in the collections of the big museums in Europe and the United States. The present paper presents the records of the five species of the genus *Calcarmyobia* taken during the trip to add to the knowledge of the mites themselves and their host taxonomy.

The abbreviations for the museums, where the material dealt with in the present paper was collected, are as follows: AMNH—American Museum of Natural History, New York; BMNH—British Museum (Natural History), London; BSPM—Bernice P. Bishop Museum, Honolulu; FMNH—Field Museum of Natural History, Chicago; MNHN—Museum National d'Historie Naturelle, Paris; RMNH—Rijksmuseum van Natuurlijke Histoire, Leiden; SMF—Forschungs—Institut Senkenberg, Frankfurt.

Records of mites

Calcarmyobia rhinolophia (Radford, 1940)

Myobia rhinolophia Radford, 1940, *Parasitol.*, **32:** 91.
Calcarmyobia rhinolophia (Radford, 1940), Radford, 1952, *Bull. Mus. Hist. Nat., Paris.*, **24:** 371; Fain, 1978, *Ann. Mus. r. Afr. cent., (Sci. Zool.)*, **224:** 92; Uchikawa, 1982, *Annot. zool. Japon.*, **55:** 32.

This species was described originally on the material taken from a number of bats by G. H. E. Hopkins and T. H. E. Jackson in a cave at Kapretwa, Mt Elgon, Kenya (Radford, 1940). The host was given as 'a bat (*Rhinolophus lobatus* Peters)', but any bat of the genus *Rhinolophus* is not a true host of *Calcarmyobia*. With the guidance of Mr John Edwards Hill, Mammal Section, British Museum (Natural History), the present author located 2 series of bat specimens collected by Hopkins and Jackson at Kapretwa in 1938 and 1940. As Radford's manuscript dealing with *Myobia rhinolophia* was received for publication on 31 October 1939, the mites had presumably been obtained from the bats caught in 1938. The bats labelled *M. natalensis arenarius* with BMNH 1938.5.10.10–14 and 1938.5.10.4–9 for *Rhinolophus lobatus* yielded a male (1984.6.12.11)

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*Supported financially by Overseas Scientific Research Grant Nos. 57041019 and 5803013 from the Ministry of Education, Science and Culture, Japan. Contribution No. Ac-2.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(1): 15–25 Issued 28 February 1985

and 2 females (1984.6.12.10) of *C. rhinolophia*. Thus, a bat (*Rhinolophus lobatus* Peters) in Radford is better to be revised as *Miniopterus natalensis arenarius* Heller. In passing, the bats of the genus *Rhinolophus* are specific hosts of the mites of the genus *Neomyobia*, and Radford (1940) also described a *Neomyobia* under the name of *Myobia jacksoni* in the same paper.

The specimens of *C. rhinolophia* taken in the present study are listed in Table 1.

Table 1 Records of *Calcarmyobia rhinolophia* (Radford)

Codes No. Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#79 1♀		*Miniopterus* sp.	Sudan	USNM 252716
#3 1♂1♀		*M. fuscus fraterculus*	Natal, S. Africa	AMNH 245207
#61 1♂3♀♀	1984.6.12.1–3	*M. inflatus africanus*	Kenya	BMNH 75.898–906
#45 2♂♂1N		*M. natalensis arenarius*	Mt Elgon, Kenya	FMNH 67958–65
#46 2♂♂3♀♀		*M. natalensis arenarius*	Mt Menengai, Kenya	FMNH 85467–78
#42 2♂♂5♀♀1N	1984.6.12.4–9	*M. natalensis arenarius*	Mt Elgon, Kenya	BMNH 36.3.16.13–20
#44 1♂2♀♀	1984.6.12.10–11	*M. natalensis arenarius*	Kapretwa, Mt Elgon	BMNH 1938.5.10.10–14*
#45 1♂1♀	1984.6.12.12–13	*M. natalensis arenarius*	Kapretwa, Mt Elgon	BMNH 40.726–37*
#65 2♂♂1♀1N		*M. schreibersi*	S. Sudan	FMNH 108169–70
#41 2♂♂2♀♀1N		*M. schreibersi arenarius*	Mt Menengai, Kenya	FMNH 91619–706
#36 1♂1♀	1984.6.12.14–15	*M. schreibersi arenarius*	Kenya	BMNH 70.726
#41 2♂♂3♀♀2N	1984.6.12.16–24	*M. schreibersi arenarius*	Mt Elgon, Uganda	BMNH 73.527–30
#47 1♂		*M. schreibersi arenarius*	Kenya	SMF 39425
#46 1♀	1984.6.12.25	*M. schreibersi natalensis*	Rhodesia	BMNH 54.1045
#3 1♂1♀1N		*M. schreibersi natalensis*	Zambia	AMNH 89780–3

*Specimens collected by Hopkins and Jackson.

Table 2 Records of *Calcarmyobia miniopteris* (Womersley)

Code No. Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#105 3♀♀**		*Miniopterus* A	Timor	AMNH——
#148 1♂	1984.6.12.26	*M. australis minor*	S. Java	BMNH 9.1.5.428*
#164 1♂	1984.6.12.27	*M. medius*	Java	BMNH 9.1.5.462–3,5,6***
#187 2♀♀	1984.6.12.28–29	*M. fuliginosus*	Burma	BMNH 32.11.1.3
#188 1♀	1984.6.12.30	*M. fuliginosus*	India	BMNH 15.7.3.12
#38 3♂♂		*M. schreibersi*	Afghanistan	SMF 38828–30
#94 1♂	1984.6.12.31	*M. schreibersi*	China	BMNH 94.9.1.23
#91 1♂1♀	1984.6.12.32–33	*M. schreibersi*	Masuri, India	BMNH 79.11.21.177
#87 1♀	1984.6.12.34	*M. schreibersi*	India	BMNH 79.984–5
#98 1♀	1984.6.12.35	*M. schreibersi*	Ceylon	BMNH 59.5.31.66
#70 1♀		*M. schreibersi*	Thailand	USNM 294364
#1 1♂1♀		*M. schreibersi fuliginosus*	India	AMNH 208160
#61 3♂♂5♀♀		*M. schreibersi fuliginosus*	Katmandu, Nepal	SMF 58389–404
#120 1♀		*M. schreibersi fuliginosus*	Ceylon	USNM 277238–40
#155 1♀	1984.6.12.36	*M. schreibersi japoniae*	Japan	BMNH 6.1.4.22*
#55 1♂		*M. schreibersi parvipes*	China	AMNM 44656*

*Type specimen, **Tentatively identified, ***Specimens with the same data as those of the type of *M. medius* (BMNH 9.1.5.4624) yielded also 2 other species of *Calcarmyobia*.

Calcarmyobia miniopteris (Womersley, 1941)

Myobia miniopteris Womersley, 1941, *Rec. S. Aust. Mus.*, **7:** 52.
Calcarmyobia rhinolophia (Radford, 1940), Radford, 1952, *Bull. Mus. Hist. Nat., Paris,* **24,** 371.
Calcarmyobia japonica Uchikawa, 1976, *Annot. zool. Japon.*, **4:** 56.
Calcarmyobia miniopteris (Womersley, 1941), Fain & Lukoschus, 1979, *Rec. West Aust. Mus.*, **7:** 72.

Calcarmyobia miniopteris (Womersley) was once synonymized with *C. rhinolopia* (Radford), but its validity was proved in 1976 by the present author, though he dealt with it as a new species. The specimens taken in the present study are shown in Table 2 and in the distribution map, Fig. 9. A male taken from the type of *M. australis minor* that has been synonymized with *M. paululus* by Maeda (1982) is thought to be a stray specimen. This will be mentioned again in the next paper.

Calcarmyobia congoensis Uchikawa, 1982

Calcarmyobia congoensis Uchikawa, 1982, *Annot. zool. Japon.*, **55:** 36.
Calcarmyobia rhinolophia (Radford, 1940), Lawrence, 1951, *Ann. Natal. Mus.*, **12:** 103.
Myobia miniopterus Womersley, 1941, Lavoipierre, 1946, *J. Entomol. Soc. S. Afr.*, **9:** 78.

Calcarmyobia congoensis Uchikawa was described from 4 male and 2 female specimens from *Miniopterus,* which were not satisfactorily identified (Ukchikawa, 1982). This species is closely allied to *C. rhinolophia* (Radford). The males of both species are, however, easily separable from each other by the structure of the genital shield and by the nature of *gp* on the shield. Compared with the inflated *gp* of *C. rhinolophia,* the seta is fine and setiform on the type specimens of *C. congoensis.*

In the present study are some 90 male specimens of the mites, which have the genital shield essentially the same in structure to that of the type specimens of *C. congoensis.* All the above specimens and their partner females have been identified as *C. congoensis,* but the particular seta *gp* shows a remarkable variation in thickness. The seta is typically setiform as in Fig. 1a on some specimens, but is obviously thickened as in Figs 1b and 1c on others. Contrary to such the clear differences in the males, the partner females of both the forms are barely separable by the nature of some setae. The striated basal part of setae d_1 and d_4 is slightly shorter on the partner females of the typical males than on those of the atypical males, and, thus, the outline of that part is

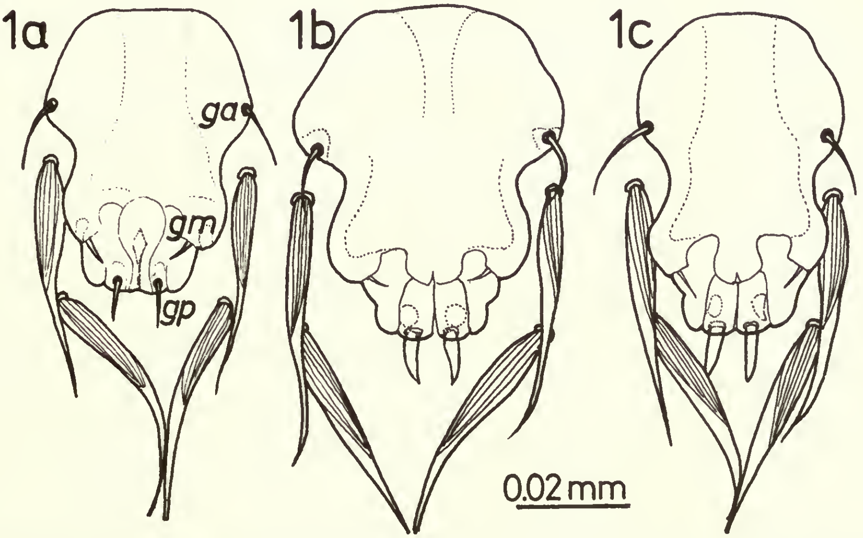


Fig. 1 Variation in thickness of the setae *gp* on the male of *Calcarmyobia congoensis* Uchikawa: typical (1a); atypical (1b & c) forms.

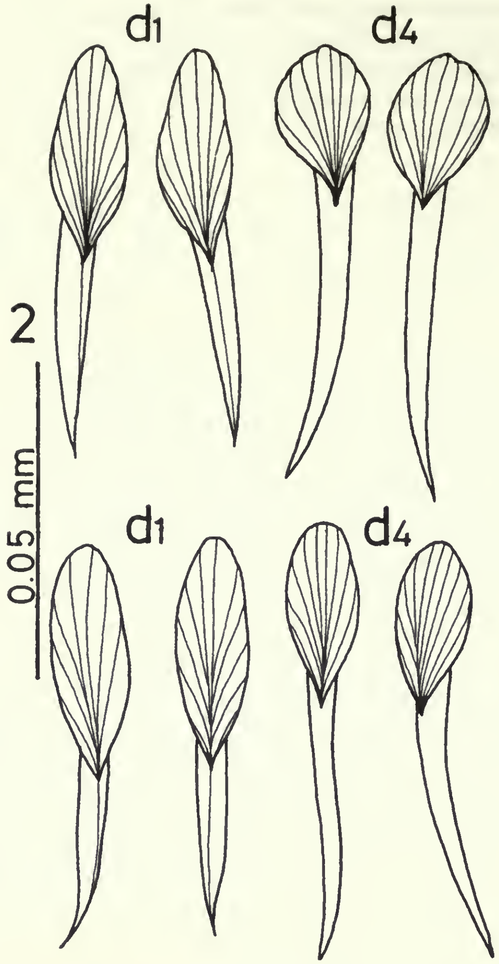


Fig. 2 Differences in the dorsal setae, d_1 and d_4, on the female of *Calcarmyobia congoensis* Uchikawa: typical (upper); atypical (lower) forms.

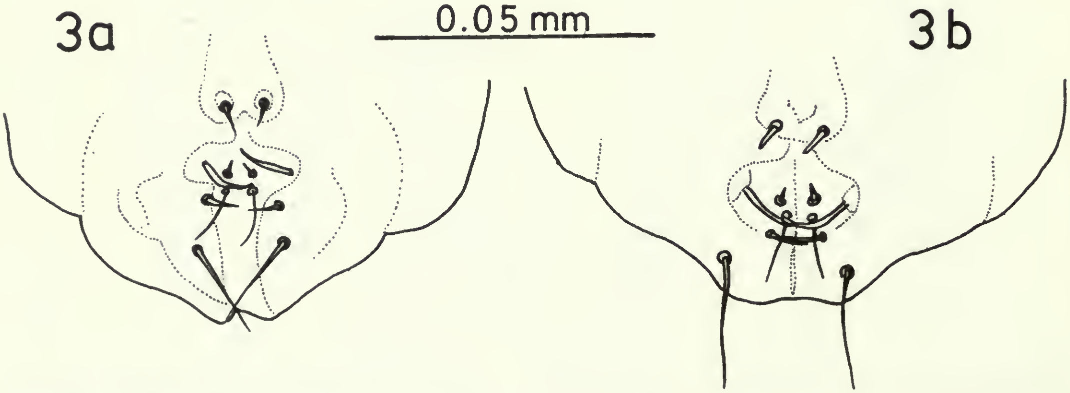


Fig. 3 Difference in the internal anal setae, *ai*, on the female of *Calcarmyobia congoensis* Uchikawa: typical (3a); atypical (3b) forms.

somewhat different in the two forms as depicted in Fig. 2. The anal seta *ai* is usually less prominent on the typical form than on the atypical form as shown in Fig. 3. According to these subtle differences in both sexes, the two forms of *C. congoensis* taken in the present study are recorded separately in Tables 3 and 4. Although both forms of the mites are regarded as being conspecific in the present study, the host and locality records in Tables 3 and 4 may be useful in consideration of the distribution pattern of the host bats and in their phylogenetic relationships.

Calcarmyobia congoensis seems to be prevailing in the Ethiopian region excluding the western part, where data are still wanting, and in Madagascar (Fig. 9). The typical form was taken frequently from the bats from the central to western parts of Africa, and the atypical form from those from Ethiopia to South Africa and just into eastern Africa. There was, however, no strict geographical segregation in the distribution of both the forms. As to the host bats, the type host of *C. congoensis, Miniopterus* from Congo (MNHN 25-05-69) is not yet properly identified. Among the host bats of the typical form in Table 2, only *M. villiersi* seems to be one of the true hosts of the mite. Some other host bats are still anonymous or to be reconfirmed as discussed later. On the other hand, the type specimens of *M. africanus, M. breyeri, M. dasythrix* and *M. scotinus* harboured the atypical form of *C. congoensis* and these species are regarded as the true hosts of the mite with the additional data in Table 3. *Miniopterus natalensis* and *M. smitianus* are also thought to be the true hosts of the atypical form of *C. congoensis.*

Lavoipierre (1946) and Lawrence (1951) recorded *Myobia miniopterus* Womersley and *C. rhinolophia* (Radford), respectively, from *M. natalensis* in Transvaal and Natal, South Africa. Their mites have not been re-examined referring to the present knowledge of *Calcarmyobia,* but it

Table 3 Records of *Calcarmyobia congoensis* Uchikawa, typical form

Code No.	Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#79	1♀		*Miniopterus* sp.	Sudan	USNM 252716
#16	1♀		*Miniopterus* sp.	Central Africa	MNHN —
#17	1♂1♀		*Miniopterus* sp.	Central Africa	MNHN —
#18	1♂2♀♀		*Miniopterus* sp.	Central Africa	MNHN —
#19	2♂♂2♀♀		*Miniopterus* sp.	Central Africa	MNHN —
#24	3♂♂1♀		*Miniopterus* sp.	Cameroun	MNHN —
#39	1♂2♀♀		*Miniopterus* sp.	Angola	FMNH 84125–37
#62	1♂1♀		*M. fraterculus*	Angola	FMNH 83601
#66	1♂	1984.6.12.37	*M. inflatus*	Belg. Congo	BMNH 59.512
♀62	1♂	1984.6.12.38	*M. inflatus africanus*	Belg. Congo	BMNH 59.513–5
#22	3♂♂7♀♀		*M. inflatus africanus*	Kenya	USNM 351059
#34	6♂4♀♀		*M. natalensis*	Mozambique	USNM 365448–52
#33	1♂		*M. natalensis*	Rhodesia	USNM 368613–4
#63	1♀		*M. natalensis*	Rhodesia	USNM 95156–7
#173	1♂2♀♀	1984.6.12.39–41	*M. schreibersi*	Angola	BMNH 4.4.9.25–6
#175	1♀	1984.6.12.42	*M. schreibersi*	Belg. Congo	BMNH 95.7.16.2
#52	2♂♂2♀♀		*M. schreibersi*	Zambia	SMF 48029–37
#49	2♀♀		*M. schreibersi arenarius*	Sudan	FMNH 68106–8
#55	11♂2♀♀		*M. schreibersi arenarius*	Kenya	SMF 19862–3
#169	1♀	1984.6.12.43	*M. schreibersi arenarius*	Kenya	BMNH 10.4.1.27
#56	4♂♂2♀♀		*M. schreibersi natalensis*	Katanga, Zaire	SMF 21300–9
#57	2♂♂3♀♀		*M. schreibersi natalensis*	Katanga, Zaire	SMF 19072–8
#47	2♀♀		*M. schreibersi natalensis*	N. Rhodesia	FMNH 96270–1
#55	1♂	1984.6.12.44	*M. schreibersi natalensis*	Zaire	BMNH 74.512–6
#84	4♀♀	1984.6.12.45–48	*M. schreibersi villiersi*	Cameroun	BMNH 68.647
#85	2♂♂	1984.6.12.49	*M. schreibersi villiersi*	Cameroun	BMNH 68.330–1
#165	1♀	1984.6.12.50	*M. schreibersi villiersi*	Cameroun	BMNH 60.106–7
#66	1♂3♀♀		*M. schreibersi villiersi*	Cameroun	FMNH 42587–90
#10	1♂2♀♀		*M. schreibersi villiersi*	?	AMNH 49321

is highly probable that they had dealt with the same species of mite. The mite is thought not to be other than the atypical form of *C. congoensis* from Tables 3 and 4.

Calcarmyobia dusbabeki nom. nov.

Calcarmyobia rhinolophia (Radford, 1940), Dusbábek, 1963, *Acta. Soc. ent. Cèchoslov.*, **60:** 248; Uchikawa, 1976, *Annot. zool. Japon.*, **49:** 57; Fain & Aellen, 1979, *Rev. suisse Zool.*, **86:** 218.

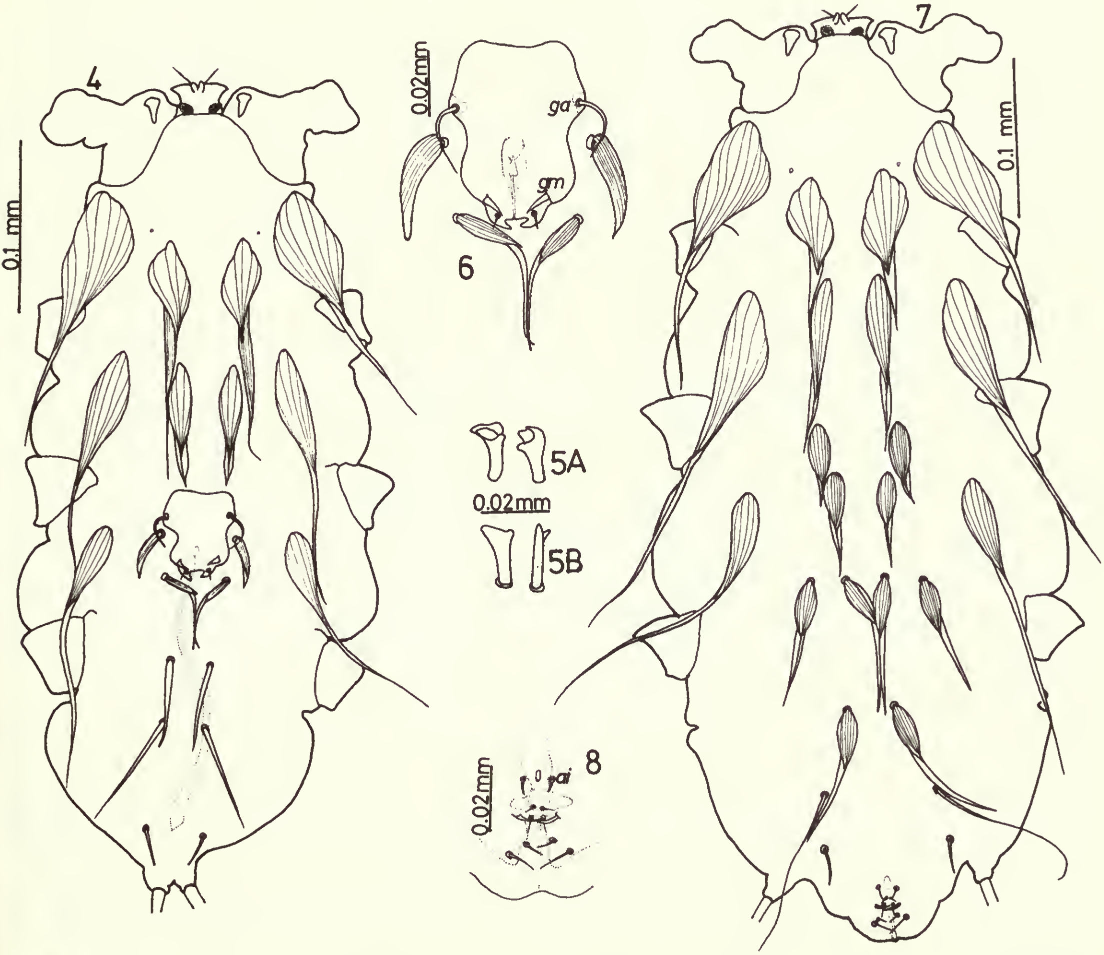
?*Calcarmyobia parenzani* Lombardini, 1956, Fain & Aellen, 1979, *Rev. suisse Zool.*, **86:** 218; Fain & Lukoschus 1979, *Rec. West Aust. Mus.*, **7:** 70: *Uchikawa, 1982, Annot. zool Japon.*, **55:** 35.

Table 4 Records of *Calcarmyobia congoensis* Uchikawa, atypical form

Code No.	Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#80	1♂		*Miniopterus* sp.	Rhodesia	USNM 154587
#83	1♂2♀♀		*Miniopterus* sp.	Transvaal	USNM 237550–4
#61	2♂♂2♀♀3N		*M. africanus*	Ethiopia	FMNH 28765,–7–8,770*
#185	1♂	1984.6.12.51	*M. africanus*	Big Abbai	BMNH 28.1.11.29–30
#182	1♂3♀♀	1984.6.12.52–55	*M. breyeri*	Transvaal	BMNH 9.7.2.3–5,7–8
#150	1♀	1984.6.12.56	*M. breyeri*	Transvaal	BMNH 9.7.2.6*
#122	2♂♂2♀♀		*M. breyeri vicinior*	Aba, Zaire	AMNH 49021,–25
#2	2♀♀		*M. breyeri vicinior*	Aba, Zaire	AMNH 49031
#14	4♂♂ 11♀♀22N		*M. dasythrix*	Caffrérie, S. Africa	RMNH 25093*
#18	2♂♂2♀♀		*M. fraterculus*	Transvaal	USNM 342641
#19	1♂2♀♀		*M. fraterculus*	S. Africa	USNM 381629,–32–4
#6	4♀♀		*M. fuscus fraterculus*	Mozambique	AMNH 216228
#44	1♂1♀		*M. inflatus*	Kenya	SMF 43660
#63	3♂♂	1984.6.12.57–59	*M. inflatus africanus*	Ethiopia	BMNH 70.492
#65	2♀♀	1984.6.12.60	*M. inflatus africanus*	Ethiopia	BMNH 72.246–87
#71	1♂2♀♀	1984.6.12.61–63	*M. inflatus africanus*	Ethiopia	BMNH 71.606–15
#24	1♂2♀♀		*M. inflatus africanus*	Kenya	USNM 436816–35
#4	1♂1♀		*M. minor fraterculus*	S. Africa	AMNH 116091
#47	1♂	1984.6.12.64	*M. natalensis*	Transvaal	BMNH 49.722
#48	5♂♂1♀	1984.6.12.65–70	*M. natalensis*	S. Africa	BMNH 52.1364–74
#51	1♀	1984.6.12.71	*M. natalensis*	Rhodesia	BMNH 62.2099–100
#53	1♂	1984.6.12.72	*M. natalensis*	Transvaal	BMNH 51.729–32
#54	1♂1♀	1984.6.12.73	*M. natalensis*	Natal	BMNH 51.21–6
#119	1♀		*M. natalensis*	Natal	AMNH 245208
#152	3♀♀		*M. natalensis*	Transvaal	BSPM 145607–8
#62	1♀		*M. natalensis*	Kenya	USNM 317129–28
#67	1♂		*M. natalensis*	Kenya	USNM 166591,–93
#92	2♂♂6♀♀	1984.6.12.74–81	*M. schreibersi*	Transvaal	BMNH 9.7.2.27–8
#65	4♂♂3♀♀		*M. schreibersi*	S. Africa	USNM 479536–7
#40	3♀♀	1984.6.12.82–83	*M. schreibersi arenarius*	Ethiopia	BMNH 72.4447–8
#46	1♂		*M. schreibersi arenarius*	Ethiopia	SMF 45735
#31	1♂1♀		*M. schreibersi arenarius*	Kenya	FMNH 182697
#36	1♀		*M. schreibersi natalensis*	Transvaal	USNM 156337
#37	1♂2♀♀		*M. schreibersi natalensis*	Transvaal	USNM 221423–30
#21	2♂♂8♀♀		*M. schreibersi natalensis*	Botswana	RMNH 30694
#23	3♂♂7♀♀		*M. schreibersi natalensis*	Botswana	RMNH 30693
#38	2♂♂		*M. schreibersi natalensis*	S. Africa	USNM 376762
#40	1♀		*M. schreibersi natalensis*	S. Africa	USNM 381599–606
#58	1♂		*M. schreibersi natalensis*	Transvaal	SMF 44807
#151	1♀	1984.6.12.84	*M. scotinus*	Caffraria, S. Africa	BMNH 46.6.2.19*
#174	2♀♀	1984.6.85	*M. scotinus*	Salisburg, Rhodesia	BMNH 95.7.16.1–2
#171	1♂1♀	1984.6.12.86–87	*M. smitianus*	S. W. Africa	BMNH 35.1.6.41–2
#172	1♂2♀♀	1984.6.12.88–90	*M. smitianus*	S. W. Africa	BMNH 35.9.1.83

*Type specimen(s).

The mite of the genus *Calcarmyobia* found in Europe was first identified as *C. rhinolophia* (Radford) by Dusbábek (1963), and, then, was proved to be a species distinctly different from the Japanese form, based on the definite criteria for differentiating species of *Calcarmyobia* (Uchikawa, 1976). Fain & Lukoschus (1979) suggested that *C. parenzani,* inadequately described by Lombardini (1956), might probably become valid as representing the populations parasitizing *M. schreibersi* in Europe. Uchikawa (1982) once followed them, but is now of the opinion that *C. parenzani* Lombardini does not represent the genus *Calcarmyobia,* and that the mite should be named on the designation of the type specimens (Uchikawa, 1984). In the present study, the specimens were found on the bats from Romania, the type locality of *M. schreibersi.* A brief description of *C. dusbabeki* nom. nov. is given below based on these specimens as the types.



Figs 4–8 *Calcarmyobia dusbabeki* nom. nov.: male dorsum (4); modified claw on leg II (5a); modified seta on tibia II (5b); genital shield and setae d_1 and d_2 (6); female dorsum (7); genito-anal setae (8).

MALE (Figs 4, 5 & 6). Setae *vi* tapering; d_1 flattened. Genital shield bearing spiniform *gm,* which are situated close to terminal lobes; genital pore slightly anterior to level of *gm.* Modified claw on leg II and modified seta, *al*, on genu II as in Fig. 5. A ventral seta on tarsus II long and thick.

Measurements in µm for holotype and, in parentheses, for two paratypes. Body (gnathosoma + idiosoma) 470 (470–490) long by 210 (215–220) wide. Setae *ve* 145 (140–133); *vi* 138 (?–140); *sc e* ?(160–165);

Table 5 Records of *Calcarmyobia dusbabeki* nom. nov.

Code No. Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#51 4♂♂4♀♀2N		*M. schreibersi*	Afghanistan	FMNH 110911–3
#11 5♀♀		*M. schreibersi*	Ukraina, USSR	AMNH 244266
#37 2♂♂3♀♀2N		*M. schreibersi*	Afghanistan	SMF 38835–9
#53 1♂1♀		*M. schreibersi*	Tunisia	SMF 22221–31
#88 3♀♀	1984.6.12.91–93	*M. schreibersi*	Tunisia	BMNH 79.918–24
#101 1♀	1984.6.12.94	*M. schreibersi*	Syria	BMNH 46.247
#103 4♀♀	1984.6.12.95–96	*M. schreibersi*	Iran	BMNH 14.39–41
#105 1♂3♀♀1N	1984.6.12.97–100	*M. schreibersi*	Iran	BMNH 14.26–38
#145 1♂7♀♀36N	1984.6.12.101–109	*M. schreibersi pallidus*	Iran	BMNH 7.7.14.7*
#28 2♂♂3♀♀		*M. schreibersi*	Algeria	RMNH 28528
#16 1♂1N		*M. schreibersi*	Algeria	RMNH —
#31 3♂♂2♀♀1N		*M. schreibersi*	Rumania	RMNH 28708–14

*Type specimen.

Table 6 Records of *Calcarmyobia kenyaensis* Uchikawa

Code No. Mites	BMNH Accession Number	Host	Locality	Host Accession Number
#84 2♂♂2♀♀1N		*Miniopterus* sp. (2spp.?)	Kenya	USNM 351247–59
#154 1♂2N	1984.6.12.110–111	*M. inflatus*	Cameroun	BMNH 3.2.4.8*
#70 1♂	1984.6.12.112	*M. inflatus*	Liberia	BMNH 79.520
#40 2♂♂2♀♀		*M. inflatus*	Katanga, Congo	SMF 21310–2
#41 1♀		*M. inflatus*	Belg. Congo	SMF 18926–7
#42 1♂2♀♀		*M. inflatus*	Kenya	SMF 39423–4
#17 2♀♀		*M. inflatus africanus*	Kenya	USNM 351014–5
#23 3♂♂1♀1N		*M. inflatus africanus*	Kenya	USNM 351040–1
#9 1♂1♀1N		*M. inflatus rufus*	Uganda	AMNH 184358–9
#45 1♂		*M. natalensis arenarius*	Kenya	FMNH 67958–65
#97 1♂	1984.6.12.113	*M. schreibersi*	Belg. Congo	BMNH 60.112
#47 2♂♂		*M. schreibersi arenarius*	Kenya	SMF 39425
#28 2♂♂1♀		*M. schreibersi arenarius*	Kenya	USNM 436845–58
#31 3♀♀		*M. schreibersi arenarius*	Kenya	USNM 182697

*Type specimen.

sc i 73 (75–77); d_1 35 (30–35); d_2 45 (43–44); d_3 50 (43–45); l_1 160(165–165); l_3 70 (?–?). Genital shield 53(50–53) long; *ga–ga* 37(37–38). Setae *al* on genu II 18(18–20) long.

FEMALE (Figs 7 & 8). Setae d_1 terminating abruptly; its membraneous tail shorter than proximal striated part. Setae on genito-anal region as in Fig. 8; g_5 distinctly shorter than g_7; *ai* setiform.

Measurements in µm for allotype and a paratype. Body 590–605 long by 270–260 wide. Setae *ve* 168–165; *vi* 105–105; *sc e* 188–190; *sc i* 108–107; d_1 53–38; d_2 63–78; d_3 90–95; d_4 90–98; l_1 200–202; l_2 85–90; d_1–d_1 50–50; d_2–d_2 30–30; d_3–d_3 22–23; l_2–l_2 70–73.

TYPES. Holotype male, allotype female, 2 paratype males and a paratype female ex *Miniopterus schreibersi*, cave near Tirgussor, Romania, 24-May-1971 (RMNH 28708–14). The types are deposited in the collection of RMNH.

The other specimens of *C. dusbabeki* nom. nov. examined in the present study are listed in Table 5. This mite was found only on *M. schreibersi* from the circum-Mediterranean regions east

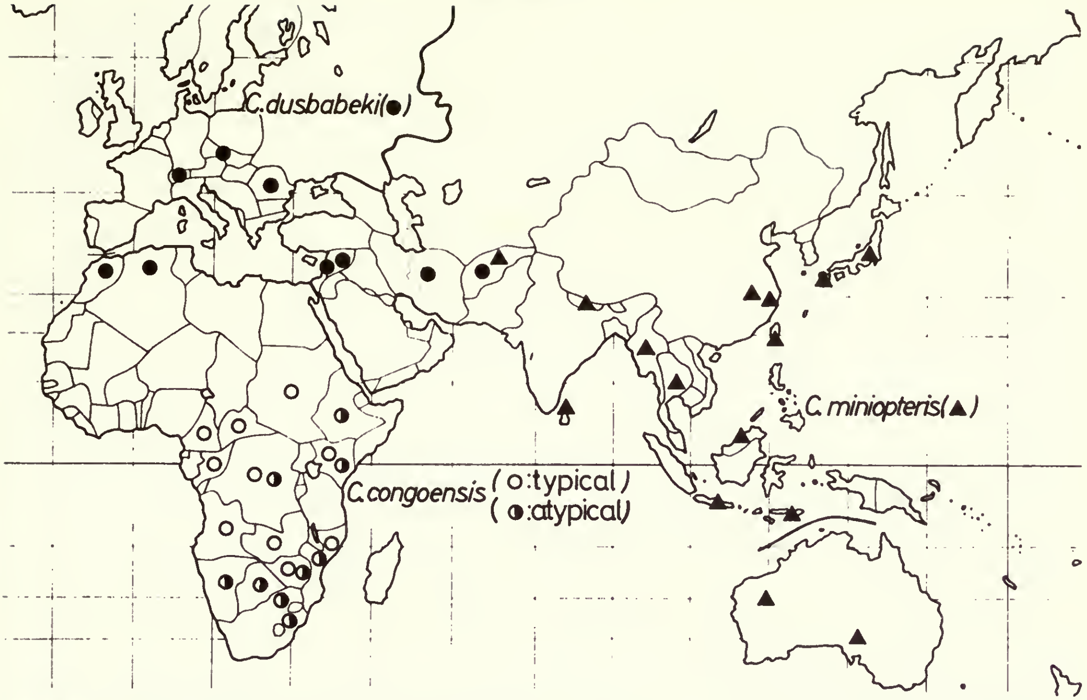


Fig. 9 The distribution of *Calcarmyobia dusbabeki* nom. nov., *Calcarmyobia miniopteris* (Womersley, 1941) and *Calcarmyobia congoensis* Uchikawa, 1982.

to Afghanistan, where the distribution of the mite met that of *C. miniopteris* (Tables 2 & 5). The distribution map of *C. dusbabeki, C. congoensis* and *C. miniopteris* based on the present data and those in Uchikawa (1983) is shown in Fig. 9. It is noteworthy that *C. dusbabeki* nom. nov. is closer to *C. congonensis* and other Ethiopian mites described than to *C. miniopteris*, the representative in the eastern Palearctic, Oriental and Australasian regions, in having the genital setae *gm* on the genital shield and an inflated ventral seta on tarsus II in the male.

Calcarmyobia kenyaensis Uchikawa, 1982

Calcarmyobia kenyaensis Uchikawa, 1982, *Annot. zool. Japon.*, 55: 37.

This mite was originally described as a parasite of *Miniopterus inflatus* from Kenya. Further records obtained in the present study are presented in Table 6. These include a male found on the type skin specimen of *M. inflatus* in the BMNH.

Discussion

The solutions to the three problems concerning the known species of the genus *Calcarmyobia* (Uchikawa, 1984) have been obtained in the present study. The first is that the host of *C. rhinolophia*, the generic type, is presumed to be *Miniopterus natalensis arenarius*. The second is that records of *Myobia miniopterus* and *C. rhinolophia* from *M. natalensis* in South Africa (Lavoipierre, 1946; Lawrence, 1951) are now thought to be the atypical form of *C. congoensis*. Finally, the well known but unnamed *Calcarmyobia* distributed in Europe has been described and type specimens designated.

The geographical distribution of some mites of the genus *Calcarmyobia* has been further established with accumulation of the data in the present study. *Calcarmyobia congoensis* with a remarkable intraspecific variation prevails in almost the whole of the Ethiopian region on various bats, inclusive of the types of *M. africanus, M. breyeri, M. dasythrix* and *M. scotinus*, as shown in Tables 3 and 4. *Calcarmyobia dusbabeki* nom. nov. is, on the other hand, distributed in the western Palearctic region east to Afghanistan, where it meets with *C. miniopteris* occurring in the eastern Palearctic, Oriental and Australasian regions (Fig. 9). Data for *C. rhinolophia* and *C. kenyaensis* are still fragmentary, yet ranges for these mites seem not to be so wide as those of the above species. Such limited distribution pattern of the mites may suggest groupings of their host bats.

The host bats of the five mite species considered in this paper are recorded in Tables 1 to 6 according to the labels in the respective collections. As the mites of the genus *Calcarmyobia* are oligoxenic and not synhospitalic (Uchikawa & Harada, 1981), it is likely for a mite to parasitize all subspecies of a bat, and for a host bat to harbour only a single species of the mites. Many host records in the tables are, however, against this rule. The present author expects that information deduced exclusively from the mites will draw attention to contradictory points in the host taxonomy.

Miniopterus schreibersi appears in all tables, suggesting a most unsatisfactory definition of this species. The mite *C. dusbabeki* parasitic on *M. schreibersi* in Europe, the type locality of the bat, has a rather limited range only in the western Palearctic region as shown in Table 5 and Fig. 9. It is therefore reasonable to regard *M. schreibersi* and its close relatives, the hosts of *C. dusbabeki*, as the bats distributed in a range similar to that of their common parasite. If this is the case, *schreibersi* in Tables 1–4 and 6 will need to be revised.

As shown in Table 1, *M. natalensis arenarius* is thought to be the true holst of *C. rhinolophia*, while *M. natalensis* is one of the common hosts of *C. congoensis* as seen in Tables 3 and 4. Although *C. rhinolophia* and *C. congoensis* are very close to each other, reflecting a close affinity among their hosts, it is improbable that different subspecies of a bat would harbour specific mites of the genus *Calcarmyobia*. Thus, *arenarius* originally described as a subspecies of *M. natalensis* should be elevated to a full species or be transferred to a subspecies of a species other than *M. natalensis*.

M. africanus, the paratypes of which yielded the atypical form of *C. congoensis*, is sometimes ranked as a subspecies of *M. inflatus* (Tables 3 & 4). As the type and other specimens of *M. inflatus* frequently harboured *C. kenyaensis* (Table 6), *M. inflatus* is believed to be a true host of *C. kenyaensis*, and, then, the host of *C. congoensis* should not be treated as a subspecies of the host bat of *C. kenyaensis*.

All six tables contain host records that are contradictory to our main premise. Some mites might have been transferred to the wrong hosts before the present author examined them, and, in some cases, misidentification might have been made for some bats even in the collections of the leading museums.

Acknowledgements

Gratitude is expressed to the curators and other staffs of the Mammal Sections of all the Museums listed above for allowing the author to examine the bats deposited in their collections for ectoparasites. Thanks are also due to Mr John Edwards Hill, Mammal Section, British Museum (Natural History), for pertinent suggestions on the bats collected by G. H. E. Hopkins and T. H. E. Jackson and Mr K. H. Hyatt for critical reading of the manuscript.

References

Dusbábek, F. 1963. Parasitische Fledermausmilben der Tschechoslowakei. III. Fam. Myobiidae (Acarina, Trombidiformes). *Acta. Soc. ent. Céchoslov.* **60:** 231–251.

Fain, A. 1978. Les Myobiidae d'Afrique au sud du Sahara et de Madagascar (Acarina, Prostigmata). *Ann. Mus. r. Afr. Cent., Sci. zool.* **224:** 1–186.

—— **& Aellen, V.** 1979. Les Myobiidae (Acarina, Prostigmata) parasites des chauves-souris de Suisse. I. *Revue suisse Zool.* **86:** 203–220.

—— **& Lukoschus, F.** 1979. Parasites of western Australia. VI. Myobiidae parasitic on bats (Acarina: Prostigmata). *Rec. West. Aust. Mus.* **7:** 61–107.

Lavoipierre, M. 1946. New records of Acari from Southern Africa and the Belgian Congo. *J. Entomol. Soc. S. Afr.* **9:** 78–81.

Lawrence, R. F. 1951. New fur-mites from South African mammals. *Ann. Natal Mus.* **12:** 91–133.

Radford, C. D. 1940. Notes on some new species of parasitic mites. Part 3. *Parasitol.* **32:** 91–104.

—— 1952. A revision of the fur mites Myobiidae (Acarina) *(Suite). Bull. Mus. Hist. Nat., Paris* **24:** 371–381.

Uchikawa, K. 1976. Myobiid mites (Acarina, Myobiidae) parasitic on bats in Japan. I. Genus *Calcarmyobia* Radford, 1952. *Annot. zool. Japon.* **49:** 55–59.

—— 1982. Mites of the genera *Calcarmyobia* and *Pteracarus* (Trombidiformes, Myobiidae) parasitic on *Miniopterus* (Chiroptera). *Ibid.* **55:** 32–45.

—— 1984. Revision of the genus *Calcarmyobia* Radford (Trombidiformes, Myobiidae) and application of the mites to the systematics of their hosts (Chiroptera), *In* Griffiths, D. A. & Bowman, C. E., (Eds.) *Acarology* VI, Vol. 1, pp. 196–201. Ellis Harwood, Chichester.

—— **& Harada, M.** 1981. Evaluation of bat-infesting Myobiidae (Acarina, Trombidiformes) as indicators in taxonomy and phylogeny of host bats (Chiroptera). *Zoo. Mag.* **90:** 351–361.

Womersley, H. 1941. Notes on the Cheyletidae (Acarina, Trombidoidea) of Australia and New Zealand with descriptions of new species. *Rec. Austral. Mus.* **7:** 51–64.

Manuscript accepted for publication 4 July 1984

Calcarmyobia from the Oriental and Australasian regions (Acarina, Myobiidae)*

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Introduction

Through examination of the *Miniopterus* bats deposited in the big museums in Europe and the United States, it is learned that mites of the genus *Calcarmyobia* specific to the genus *Miniopterus* have accomplished more advanced speciation in the Oriental and Australasian regions than in the Ethiopian region, and that all the species of mites from the Oriental and Australasian regions have in common some morphological properties that are different from those shared by the species from the Ethiopian region. The present paper deals with the description and records of mites from Oriental and Australasian *Miniopterus.*

Three species of these mites, *C. miniopteris* (Womersley), *C. hamata* Uchikawa *et al.* and *C. australasiae* Fain and Lukoschus, have so far been described from *Miniopterus* in the Oriental and Australasian regions. Twelve new taxa, inclusive of the six new subspecies, are found in the present study, and the number of species and subspecies of *Calcarmyobia* from these regions is now fifteen. As the records of *C. miniopteris* were already presented in the preceding paper (Uchikawa, 1985*a*), the other 14 taxa will be described below.

All the specimens came from the bats deposited in collections of AMNH (American Museum of Natural History, New York), BALM (Basel Museum of Natural History, Basel), BSPM (Bishop Museum, Honolulu), BMNH (British Museum (Natural History), London), FMNH (Field Museum of Natural History, Chicago), MNHM (Museum National d'Histoire Naturelle, Paris), ROM (Royal Ontario Museum, Toronto), SMF (Forschungs-Institut Senkenberg, Frankfurt) and USNM (US National Museum, Washington), and they all will be returned to the acarine collections in the respective museums.

The scales for all the figures are the same to those in Figs 1–6.

Calcarmyobia orianae orianae sp. n., ssp. n.

MALE (Figs 1, 2, 3 & 4). Posterior part of setae *vi* inflated, finely striated and granulated. Setae d_1 very fine, only slightly thicker than *ga*. Genital shield lacking setae *gm* and with posterior lobes extending beyond basal level of d_2; costal formation closer to base of d_2 than to base of d_1; genital pore situated slightly posterior to basal level of d_2; *gp* stout and pointed. Modified claw on leg II slightly thinner and shorter than normal one and forked. Modified seta on genu II as in Fig. 4; no inflated or thickened setae on tarsus II.

Measurements in µm for holotype and, in parentheses, for 5 paratypes and 4 other specimens: Body (=Gnathosoma+idiosoma) 460 (460–540) long by 210 (205–235) wide. Seta *ve* 165 (167–180) long; *vi* 115 (110–115) long; *sc e* 168 (170–200) long; *sc i* 60 (58–63) long; d_1 30 (28–32) long; d_2 63 (60–70) long; d_3 55 (50–57) long; l_1 168 (155–183) long; l_3 83 (68–85) long. Genital shield 57 (58–63) long; distance between *ga, ga–ga* 34 (33–40). Modified setae on genu II 14–17 long.

FEMALE (Figs 5 & 6). Seta d_1 with tail almost the same in length to basal striate part; d_3 originating almost from or slightly anteriad from basal level of l_2, closer to each other than to l_2. Basal striated part of d_2–d_4 and l_2 rather long and spindle-shaped. Internal anal setae *ai* clavate. A pair of stout scales with blunt tips laterally on opisthosoma.

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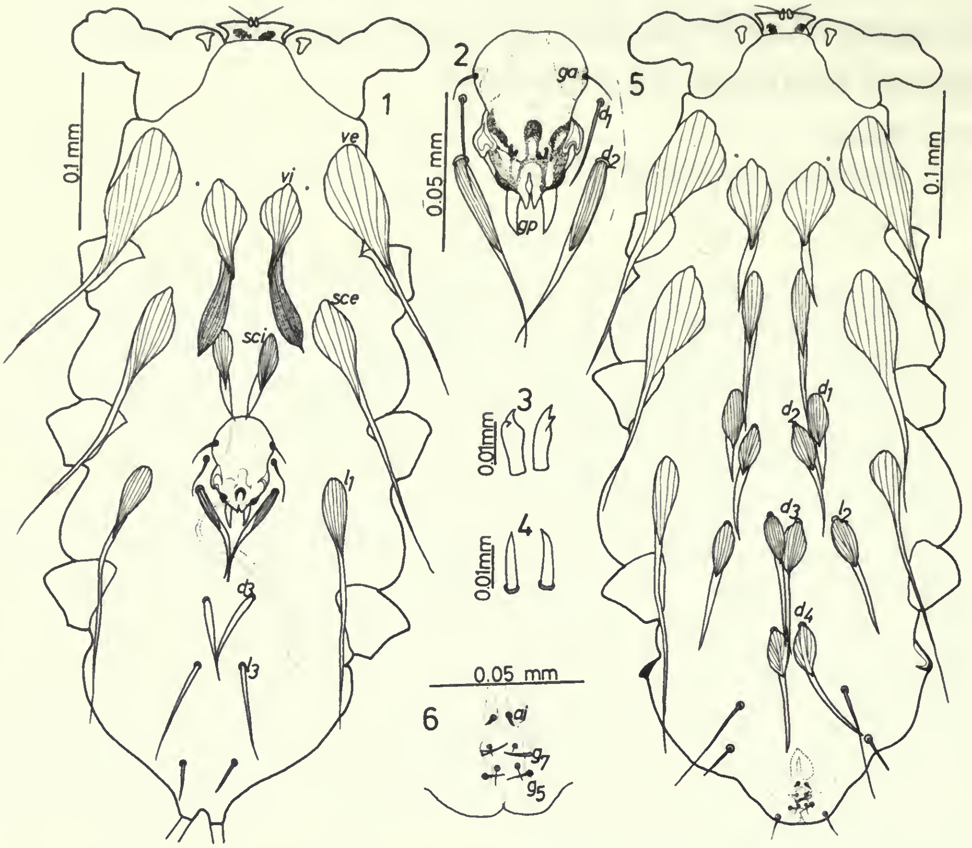
*Supported financially by Overseas Scientific Research Grant Nos. 57041019 and 5803013 from the Ministry of Education, Science and Culture, Japan. Contribution No. Ac-3.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(1): 27–44 Issued 28 February 1985



Figs 1–6 *Calcarmyobia orianae orianae* sp. n., ssp. n.: holotype male (1); genital shield of male (2); modified claw on leg II of male (3); modified seta on genu II of male (4); allotype female (5); genito-anal setae of female (6).

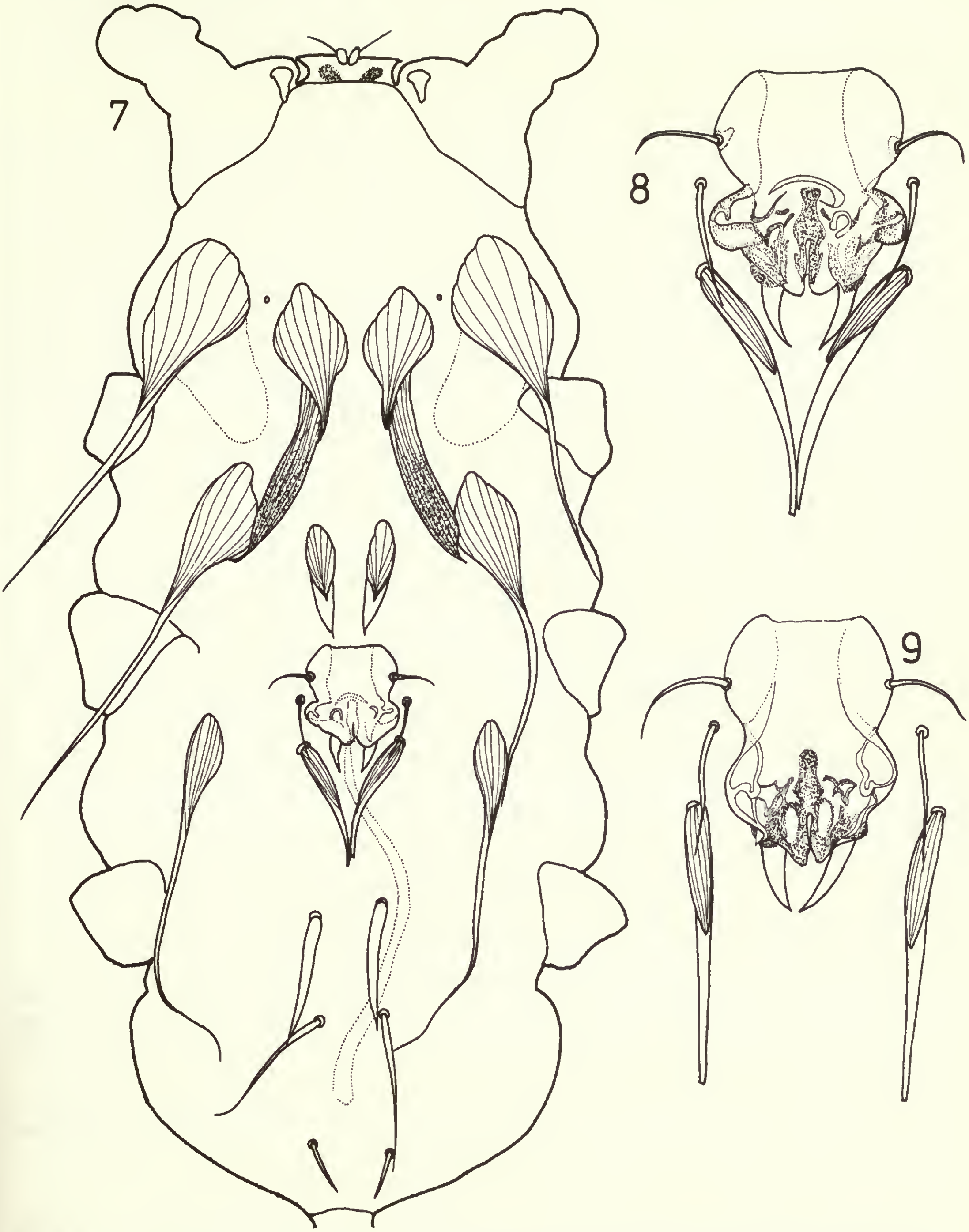
Measurements in μm for allotype and, in parentheses, for 5 other specimens. Body 545 (560–585) long by 240 (250–270) wide. Seta *ve* 173 (175–183); *vi* 104 (100–105); *sc e* 180 (188–198); *sc i* 110 (110–123); d_1 68 (58–63); d_2 75 (73–80); d_3 92 (95–98); d_4 85 (93–100); l_1 180 (185–198); l_2 90 (88–100); d_1–d_1 53 (55–62); d_3–d_3 16 (17–20); d_3–l_2 25 25–28).

MATERIAL EXAMINED. Holotype male, allotype female, 2 paratype males and a male ex *Miniopterus orianae*, Darwin, Australia, 9–IV–1948 (USNM 284209–34); 1♂ ex *M. orianae*, Wongabel, Queensland, Australia, 15–X–1946 (FMNH 60858); 1♂ ex *Miniopterus* (labelled *blepotis blepotis*), Chillagoe, Queensland, Australia, 7–I–1922 (FMNH 44245–7); 1♂ 2♀♀ ex *Miniopterus* (labelled *schreibersi*), Misima Is., Terr. Papua New Guinea, 8–VIII–1956 (AMNH 190473–8); 3♂♂ 3♀♀ ex *Miniopterus* (labelled *tibialis*), Finschhafen, Morobe Dist., Papua New Guinea, 22, 23–IX–1964 (AMNH 195333–45); 1♀ ex *Miniopterus* (labelled *magnater*). Kamu Valley, New Guinea, 18-VIII-1962 (BSPM 21608); 1♀ ex *Miniopterus* (labelled *magnater*), Morobe Dist., Papua New Guinea (BSPM 145440–3); 1♂ data uncertain (BSPS).

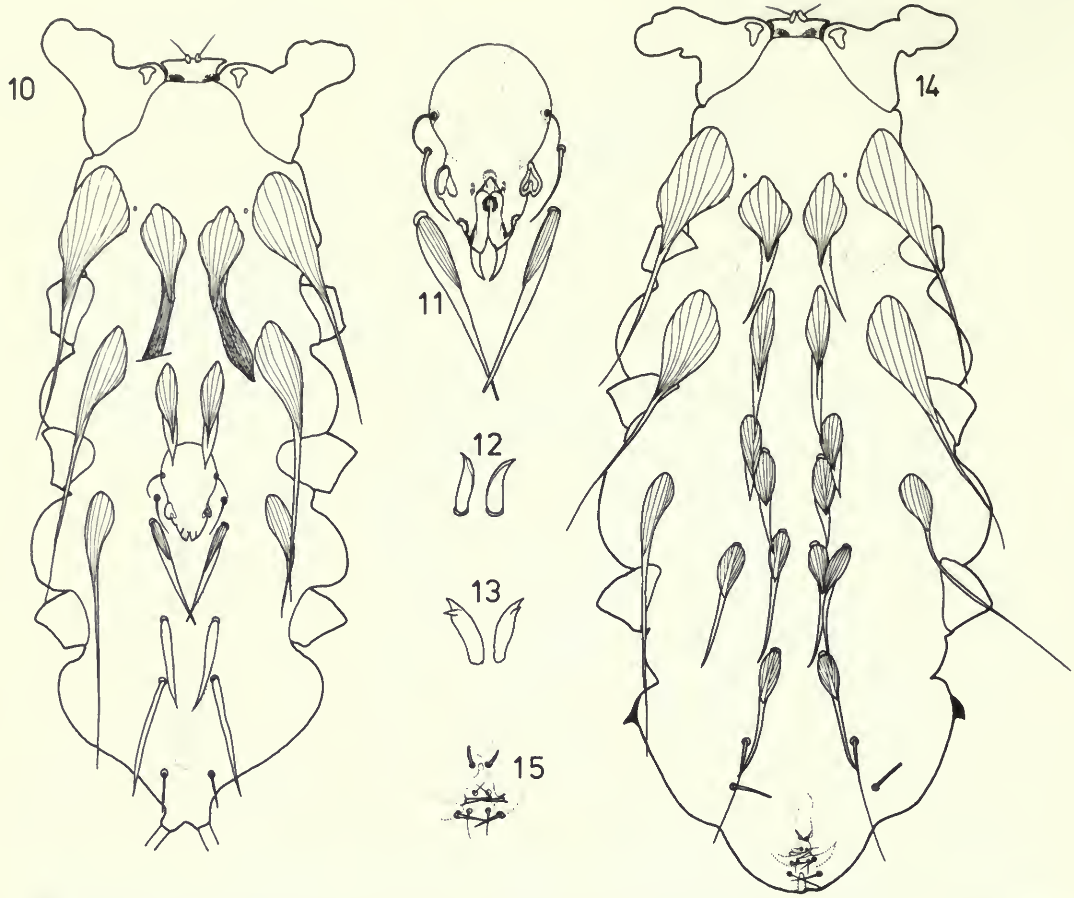
REMARKS. The present new species is characterized by the structure of the male genital shield as in Fig. 2. The female, on the other hand, shares many characteristics with those of other species.

The male shows a remarkable variation in size. The types measured 460 μm in length (Fig. 1), while others reach a length of 540 μm.

Miniopterus orianae is regarded as one of the true hosts of the mite, but the specific names of the bats listed above in parentheses are to be reconfirmed later.



Figs 7–9 *Calcarmyobia orianae eminens* ssp. n.: holotype male (7); genital shields of holotype (8) and paratype (9).



Figs 10–15 *Calcarmyobia biloba* sp. n.: holotype male (10); genital shield of male (11); modified seta on genu II of male (12); modified claw on leg II of male (13); allotype female (14); genito-anal setae of female (15).

Calcarmyobia orianae eminens ssp. n.

MALE (Figs 7, 8 & 9). Genital shield with flat anterior margin and well developed costal formation; posterior part narrowed abruptly (Figs 8–9). Seta *vi* slightly longer than that of the nominate form; *sc i* short and with broad and short tail. Other structures essentially as in the nominate form.

Measurements in µm for holotype and a paratype. Body 535–510 long by 240–? wide. Seta *ve* 175–182; *vi* 130–125; *sc e* 178–195; *sc i* 55–57; d_1 ca. 30; d_2 60–65; d_3 55–50; l_1 170–173; l_3 78–65. Genital shield 57 long (paratype); *ga–ga* 35–38. Modified seta on genu II 17–15.

FEMALE. Unknown.

MATERIAL EXAMINED. Holotype male (1984.6.12.114) and a paratype male (1984.6.12.115) ex *Miniopterus* (labelled *schreibersi*), Peradeniya, Ceylon (BMNH 13.2.10.34–7).

REMARKS. *Calcarmyobia orianae eminens* ssp. n. is based only on the two male specimens. The genital shield, bearing the most important characteristics for separating species, is different in the holotype and paratype as depicted in Figs 8 and 9. On the supposition that the shield of the holotype is deformed, the paratype is compared with the nominate form, and minor differences in the outline of the shield and the seta *sc i* of both forms is regarded as being of subspecies level.

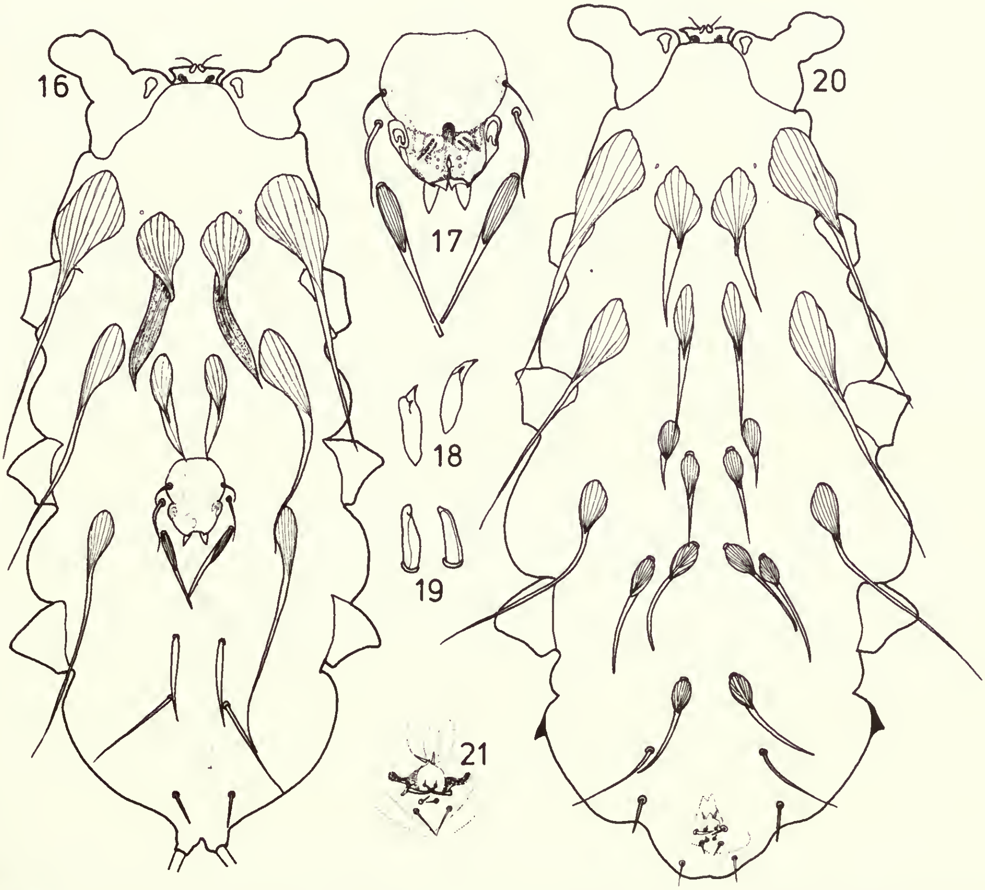
The host bats of the mite were from Ceylon, where *C. miniopteris* (Womersley) was also recorded (Uchikawa, 1985*a*).

Calcarmyobia biloba sp. n.

MALE. (Figs 10, 11, 12 & 13). Seta *vi* inflated, finely striated and granulated posteriorly. Seta d_1 fine; d_2 stout; d_3 inflated. Genital shield long and with 2 pairs of posterior lobes; anterior part oval; posterior part tapering; genital pore almost on basal level of d_2; *gp* stout and pointed apically. Modified claw on leg II forked, slightly inferior in size to normal one. Modified seta on genu II peg-like.

Measurements in µm for holotype. Body 475 long by 200 wide. Seta *ve* 178; *vi* ca. 120; *sc e* 185; *sc i* 68; d_1 28; d_2 63; d_3 52; l_1 170; l_3 80. Genital shield 62 long; *ga–ga* 35. Modified setae on genu II 15.

FEMALE (Figs 14 & 15). Seta d_1 with striated part 1.5 times as long as membranous tail; d_3 situated almost on or slightly anterior to basal level of l_2; d_3 and l_2 spaced at almost the same intervals. Lateral scales on opisthosoma strong and pointed. Genital seta g_7 slightly thicker than g_5; *ai* spiniform.



Figs 16–21 *Calcarmyobia brevis brevis* sp. n., ssp. n.: holotype male (16); genital shield of male (17); modified claw on leg II of male (18); modified seta on genu II (19); allotype female (20); genito-anal setae of female (21).

Measurements in µm for allotype and a paratype. Body 600–600 long by 265–260 wide. Seta *ve* 178–?; *vi* 105–108; *sc e* 192–178; *sc i* 120–115; d_1 58–63; d_2 78–78; d_3 92–100; d_4 90–95; l_1 188–?; l_3 90–95; d_1–d_1 60–60; d_3–d_3 23–23; d_3–l_3 25–25.

MATERIAL EXAMINED. Holotype male ex *Miniopterus macrocneme*, New Caledonia (BALM 1761, -63-6, Cotypes); allotype female and a paratype female ex *M. macrocneme*, New Caledonia, VII–XI–1944 (FMNH 55291–321).

REMARKS. *Calcarmyobia biloba* sp. n. is distinct in having the genital shield with 2 pairs of posterior lobes in the male. The female is, however, hardly separable from those that bear the lateral scales on the opisthosoma.

Calcarmyobia brevis brevis sp. n., ssp. n.

MALE (Figs 16, 17, 18 & 19). Posterior part of seta *vi* inflated, finely striated and granulated. Seta d_1 fine and much smaller than d_2. Genital shield short; posterior lobes terminating at basal level of d_2; coastal formation closer to d_1 than to d_2. Modified claw on leg II forked, slightly smaller in size than normal one. Modified seta on genu II stout and peg-like.

Measurements in µm for holotype and a paratype. Body 480–460 long by 215–210 wide. Seta *ve* 178–190; *vi* 115–113; *sc e* 163–160; *sc i* 65–63; d_1 28–25; d_2 and d_3 51–53 and 50–48, respectively; l_1 153–150. Genital shield 50–48 long; *ga–ga* 35–38. Modified seta on genu II 15–15.

FEMALE (Figs 20 & 21). Seta *sc i* short and weak; basal striated part of d_1–d_4 and l_2 short and bulbous; l_1 also inflated at base and narrowed abruptly; d_3 originating from distinctly anterior level of l_2 and slightly closer to each other than to l_2. Setae in genito-anal region not prominent; *ai* spiniform. A pair of pointed scales laterally on opisthosoma.

Measurements in µm for allotype and, in parentheses, for two paratypes. Body 575 (570–560) long by 280 (275–270) wide. Seta *ve* 190 (185-ca.183); *vi* 100 (95–105); *se e* 198 (200–210); *se i* 103 (98–102); d_1 50 (50–45); d_2 68 (67–63); d_3 83 (82–80); d_4 80 (80–88); l_1 185 (183–182); l_2 85 (80–83); d_1–d_1 55 (52–53); d_3–d_3 25 (24–25); d_3–l_2 28 (25–26).

MATERIAL EXAMINED. Holotype male, allotype female, a paratype male and 2 paratype females ex *Miniopterus* (labelled *australis pusillus*), Hubili, Dharwar, Mysore, India, 3–I–1975 (SMF 47841).

REMARKS. C. *brevis brevis* sp. n., ssp. n. is distinct in having the genital shield with short posterior part in the male. Females of the genus *Calcarmyobia* usually reveal few specific morphological properties, but *C. brevis brevis* is remarkable for the bulbous formation of the striated part of the submedian setae dorsally on the hysterosoma and for a pair of pointed lateral scales on the opisthosoma.

Calcarmyobia brevis grandis ssp. n.

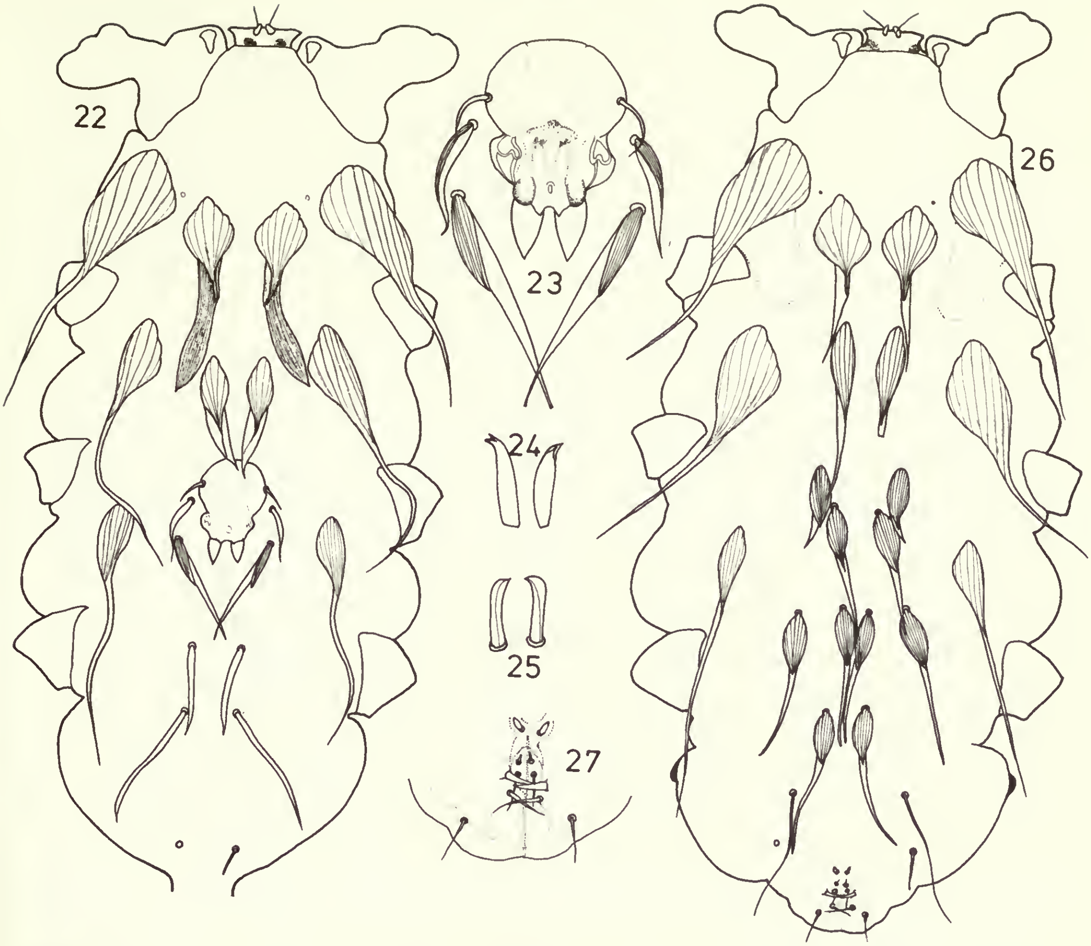
MALE (Figs 22, 23, 24 & 25). Setation, setal nature and structure of all parts essentially the same as in the nominate form, but measurements being larger. Setae *sc i*, d_1, d_2, *ga* and *gp* especially more prominent than corresponding setae of the nominate subspecies as shown in Figs 22 and 16.

Measurements in µm for holotype and, in parentheses, for three paratypes. Body 530 (530–540) long by 240 (235–250) wide. Seta *ve* 178 (175–180); *vi* 120 (128–130); *sc e* ca. 180 (170–170); *sc i* 78 (68–78); d_1 45 (45–48); d_2 70 (66–77); d_3 58 (60–65); l_1 ? (170–180); l_3 89 (85–85). Genital shield 55 (55–55) long: *ga–ga* 43 (40–43). Modified seta on genu II 18 (17–20) long.

FEMALE (Figs 26 & 27). Bases of seta d_3 almost on basal level of l_2. Striated part of d_1–d_4 and l_1 rather long and spindle-like. Anal seta *ai* clavate. Lateral scales on opisthosoma not pointed.

Measurements in µm for allotype. Body 610 long by 285 wide. Seta *ve* 183; *vi* 115; *sc e* ca. 200; *sc i* 123; d_1 60; d_2 83; d_3 88; d_4; 95; l_1 195; l_2 105; d_1–d_1 55; d_3–d_3 20; l_2–l_2 70.

MATERIAL EXAMINED. Holotype male ex *Miniopterus tristis tristis*, Philippines (ROM 43655); allotype female ex *M. tristis tristis*, Manjuryo Is., Philippines, 28–V–1966 (ROM 39860); 1♀ from the same host and locality as paratype female, 18–V–1966 (ROM 39668); 2 paratype males ex *M. tristis celebensis*, S. Sulawesi, 29–IX–1972 (AMNH 241557, type); a paratype male from *M. t. celebensis* with the same data as preceding ones (AMNH 241558).



Figs 22–27 *Calcarmyobia brevis grandis* ssp. n.; holotype male (22); genital shield of male (23); modified claw on leg II of male (24); modified seta on genu II of male (25); allotype female (26); genito-anal setae of female (27).

Calcarmyobia brevis intermedia ssp. n.

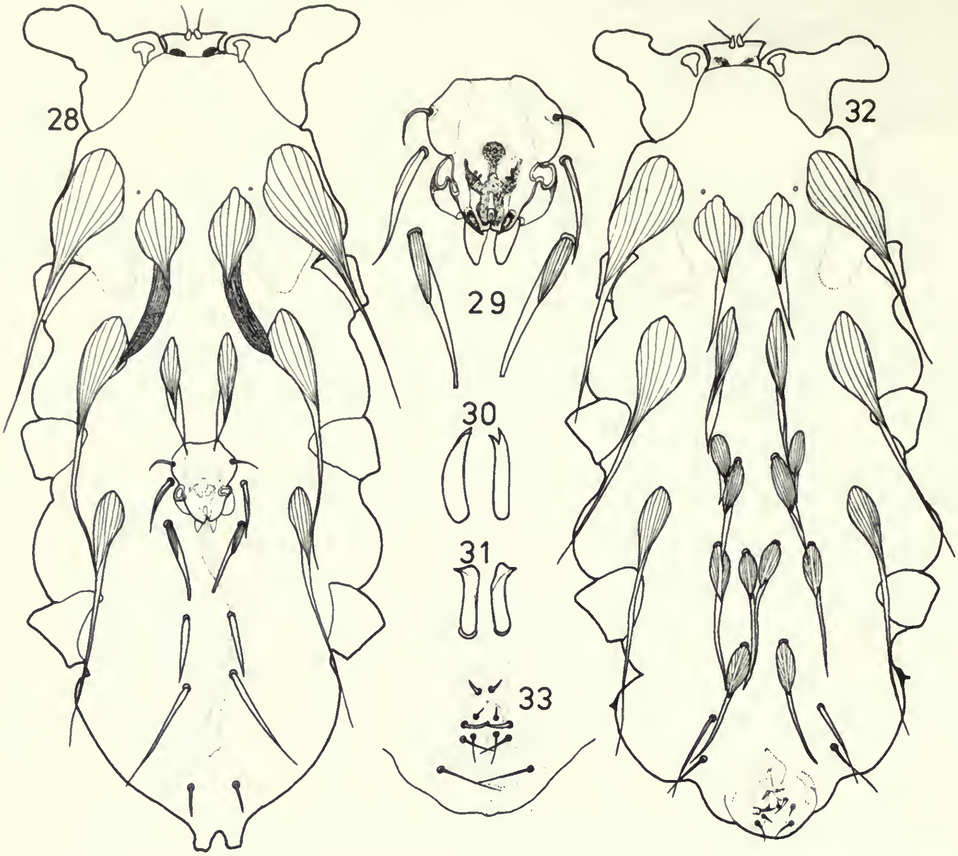
Male (Figs 28, 29, 30 & 31). Structure of genital shield and nature of setae on and flanking the shield almost the same as those of *C. brevis grandis*, but inferior in size to them.

Measurements in µm for holotype and a paratype. Body 500–490 long by 220–230 wide. Seta *ve* 173–170; *vi* 118–120; *sc e* ?–170; *sc i* 70–73; d_1 35–38; d_2 52–62; d_3 45–50; l_1 153–160; l_3 73–78. Genital shield 50–45 long; *ga–ga* 40–38. Modified seta on genu II 15–16.

Female (Figs 32 & 33). Nature of submedian setae on hysterosoma almost the same to that of *C. brevis grandis*. Lateral scales on opisthosoma not so prominent. Genital seta g_7 narrow; *ai* setiform.

Measurements in µm for allotype and a paratype. Body 540–570 long by 260–250 wide. Seta *ve* 175–175; d_2 75–175; d_2 75–83; d_3 100–95; d_4 93–93; l_1 183–180; l_3 100–105; d_1–d_1 58–60; d_3–d_3 20–20; l_2–l_2 63–70.

Material examined. Holotype male, allotype female and a paratype male and female ex *Miniopterus eschscholtzii*, Mindanao, Philippines, 19–V–1952 (FMNH 80384–431); 1♂ ex *M. eschscholtzii*, Philippines (USNM 17906).



Figs 28–33 *Calcarmyobia brevis intermedia* ssp. n.: holotype male (28); genital shield of male (29); modified claw on leg II of male (30); modified seta on genu II of male (31); allotype female (32); genito-anal setae of female (33).

REMARKS. *Calcarmyobia brevis grandis* ssp. n. and *C. brevis intermedia* ssp. n. are closer to each other than to the nominate form in having well developed d_1, d_2 and *gp* in the male. The basal striated part of the submedian setae dorsally on the hysterosoma of the female is bulbous in *C. brevis brevis* while it is spindle-like in both *C. brevis grandis* and *C. brevis intermedia*, suggesting a relative affinity among the three subspecies.

The above three subspecies are regarded as being suggestive of a phylogenetic relation among their hosts. The host bat of *C. brevis brevis, M. tristis* sspp. and *M. eschscholtzii*, may be closer to one another than to any other species of bats of the genus *Miniopterus*. This is distinctly contradictory to the knowledge gained from the general anatomy of the bats. For example, it is unusual for *M. tristis* sspp. to be considered closer to *M. eschscholtzii* than to other members of the *tritis* group in the accepted taxonomic relationships. The acarological data given above may lead to new information regarding the taxonomy of the hosts.

Calcarmyobia hamata hamata Uchikawa, Maeda, Harada & Kobayashi, 1980

Calcarmyobia hamata Uchikawa *et al.*, 1980, Contrib Biol. Labo. Kyoto Univ., **26:** 111.

Calcarmyobia hamata Uchikawa *et al.* is characterized by the structure of the genital shield, nature of d_1 and d_2, unique form of modified claw on leg II and a spiniform seta dorsally on tibia II in the male (Figs 34, 35 and 36). The female is distinct in having a pair of scales dorso-laterally on the opisthosoma. The mite was originally described from Bornean *Miniopterus schreibersi*, which has lately been reidentified by Maeda (1982) as *M. blepotis*.

Measurements in µm for holotype and 5 paratype males (Uchikawa *et al.*, 1980). Body 480 (490–500) long by 195 (195–210) wide. Seta *ve* 197 (200–210); *vi* 115 (113–123); *sc e* 173 (165–173); *sc i* 68 (70–74); d_1 35 (35–40); d_2 40 (32–38); l_1 165 (145–167). Genital shield ? (48–53) long; *ga–ga* ? (36–38). Modified claw on leg II ? (43–45) long; modified seta on genu II ? (20–20).

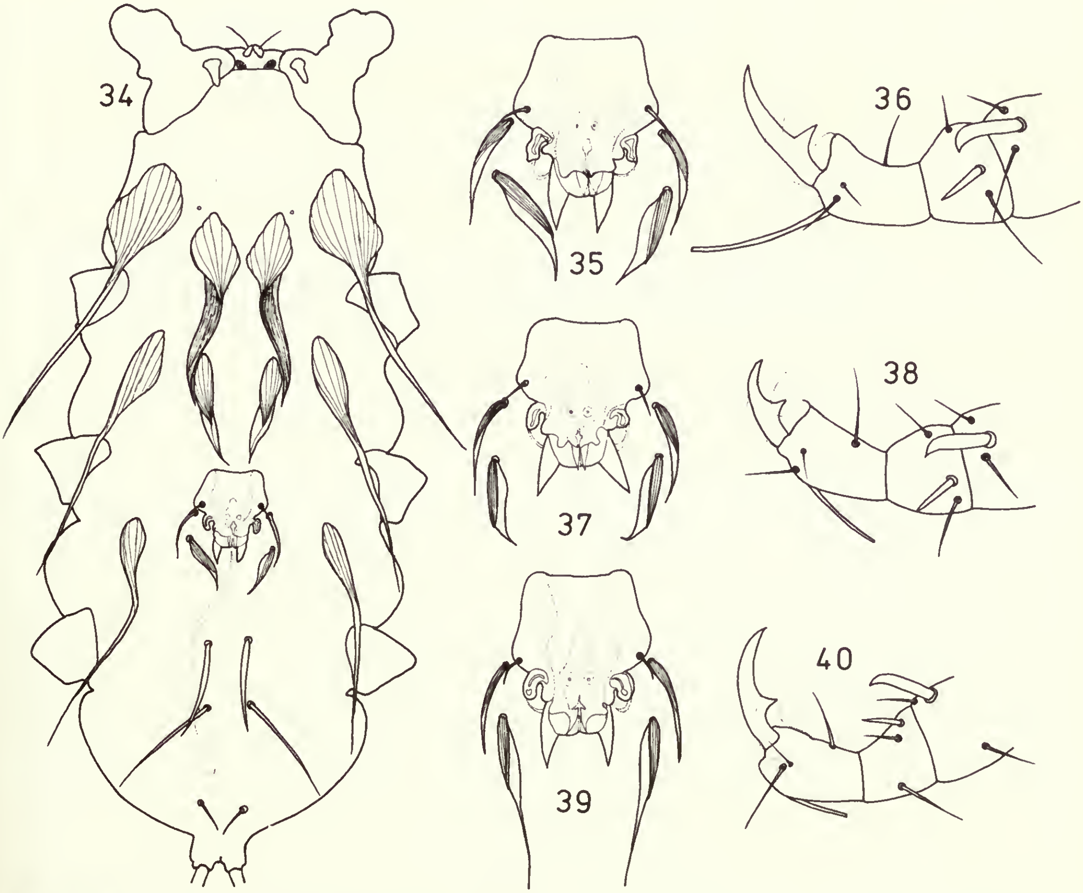
Measurements in µm for allotype and 4 paratype females (Uchikawa *et al.*, 1980). Body 585 (590–630) long by 270 (275–300) wide. Seta *sc e* 210 (200–208); *sc i* 115 (105–113); d_1 58 (55–62); d_2 70 (73–75); d_3 100 (93–97); d_4 95 (80–90); d_5 81 (75–80); l_1 204 (183–195); l_2 90 (80–88); d_1–d_1 50 (50–53); d_2–d_2 25 (24–27); d_3–d_3 ? (20–20); l_2–l_2 ? (63–68).

Calcarmyobia hamata breviungulae nom. n.

Calcarmyobia hamata Uchikawa *et al.*, 1983, *Acarologia*, **24:** 61.

MALE (Figs 37 & 38). Modified claw on leg II subequal in size and thickness to normal one; hook on modified claw small. Other structure, setation and setal nature as in nominate form.

Measurements in µm for holotype and 2 paratypes. Body 460 (465–450) long by 200 (205–200) wide. Setae *ve* 195 (200–195); *vi* 108 (115–115); *sc e* 158 (160–?); *sc i* 65 (65–63); d_1 38 (33–35); d_2 30 (33–31); d_3 40



Figs 34–40 *Calcarmyobia hamata* sspp. *C. hamata hamata* Uchikawa *et al.*: paratype male (34); genital shield of male (35); leg II of male (36). *C. hamata breviungulae* ssp. n.: genital shield of male (37); leg II of male (38). *C. hamata longisetae* ssp. n.: genital shield of male (39); leg II of male (40).

(43–42); l_1 145 (145–140); l_3 63 (70–65). Genital shield 47 (43–43) long; *ga–ga* 35 (35–33). Modified claw on leg II 25 (27–27); modified seta on genu II 20 (21–20).

FEMALE. Hardly separable from nominate form.

Measurements in µm for allotype and 2 paratypes. Body 580 (550–560) long by 255 (250–250) wide. Seta *ve* 190 (183–?); *vi* 105 (100–95); *sc e* 200 (208–195); *sc i* 100 (107–98); d_1 58 (55–50); d_2 68 (68–68); d_3 95 (88–85); d_4 83 (83–?); l_1 193 (195–190); l_3 83 (80–80); d_1–d_1 58 (50–50); d_2–d_2 25 (25–23); d_3–d_3 20 (18–18); l_2–l_2 67 (60–60).

MATERIAL EXAMINED. Holotype male, allotype female, 2 pairs of paratype males and females ex *Miniopterus haradai*, Lampang Chae Mon, Tham Husi Lang, Thailand, date uncertain; 2♂♂ from the same host and locality, 25–VI–1969; 1♂1♀ ex *M. haradai*, Ban Rai, Uthaithani, Thailand, date uncertain.

The holotype and allotype will be deposited in the collection of the National Science Museum (Nat. Hist.), Tokyo, and the other specimens in the collection of the author.

REMARKS. All the above specimens were recorded under the name *Calcarmyobia hamata* Uchikawa *et al.* in the previous paper (Uchikawa *et al.*, 1983). In the present study, the typical form of *C. hamata* was not found on any bat from the Oriental region, suggesting a limited distribution of the mite. Another form of *C. hamata* was further taken from the bats from West Java. According to the difference in the species and geographical ranges of the host bats of respective forms of the mites, such a minor but distinct deviation in the modified claw on leg II is regarded as being of a subspecific level.

The host bat of *C. hamata breviungulae* ssp. n. had long been named *Miniopterus medius* in Thailand (Hill & McNeely, 1975; Uchikawa *et al.*, 1983), but Maeda (1982) described it as a new species, *M. haradai*.

Calcarmyobia hamata longisetae ssp. n.

MALE (Figs 39 & 40). Seta d_2 gradually tapering and long. Other properties essentially as in nominate form.

Measurements in µm for holotype and 3 paratypes. Body 450 (460–480) long by 200 (195–208) wide. Seta *ve* 190 (193–195); *vi* 118 (118–120); *sc e* 170 (160–168); *sc i* 65 (68–70); d_1 31 (33–38); d_2 60 (53–58); d_3 40 (40–53); l_1 158 (153–155); l_3 66 (68–78). Genital shield 48 (45–48) long; *ga-ga* 32 (35–37). Modified claw on leg II 39 (35–50) long; modified seta on genu II 18 (18–20).

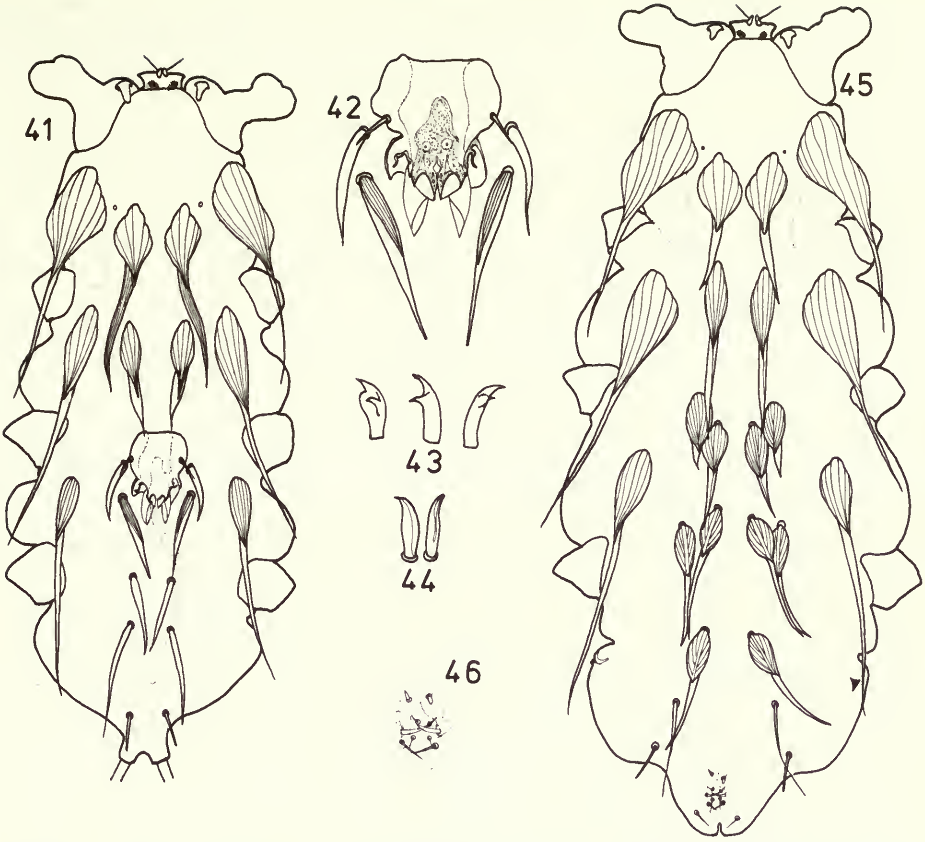
FEMALE. Seta d_1 with minute tail, but hardly separable from nominate form.

Measurements in µm for allotype. Body 570 long. Seta *ve* more than 175; *vi* 102; *sc e* 198; *sc i* 112; d_1 50; d_2 80; d_3 95; d_4 88; l_1 190; l_2 90; d_1–d_1 53; d_2–d_2 23; d_3–d_3 18; l_2–l_2 63.

MATERIAL EXAMINED. Holotype male and allotype femle *ex Miniopterus* sp., Cianjur, W. Java, 1970 (USNM 501673–87); 3 paratype males ex *Miniopterus* (labelled *schreibersi*), Campea, Bogor, W. Java, 21–VIII–1970 (USNM 501671); 1♂ (1984.6.12.116) together with *C. miniopteris* (Womersley (1♂) (1984.6.12.27) and *C. australasiae* Fain & Lukoschus (1♂1♀) (1984.6.12.126–127) ex *M. medius*, Kalipoetjang, Tjitandoei River, Java, 4–III–1908 (BMNH 9.1.5.462–3, 5–6).

REMARKS. *Calcarmyobia hamata longisetae* ssp. n. is distinctive in having the long and hooked modified claw on leg II and the seta d_2 not terminated abruptly in the male.

The full range of host bat species cannot at present be determined because the series of bats that yielded the holotype and allotype is undetermined. Although the second series of host bats was labelled *M. schreibersi*, it is reasonable to presume that *M. schreibersi* is not distributed in the Oriental region (Uchikawa, 1985*a*). The specimen USMN 501671 seems to have been taken together with *Miniopterus* sp., the hosts of the holotype and allotype of the mite. The alcoholic specimens of the type series of *M. medius* in the collection of the BMNH (9.1.5.462–3, 5–6) harboured *C. miniopteris* and *C. australasiae* as well as *C. hamata longisetae*, confirming the post-mortem transfer of mites on museum bat specimens. These bats were originally constituents of the collection made by Shortridge in Java in 1908, which also included *M. paululus* (BMNH 9.1.5.426–7, –29–43), *M. australis minor* (type, BMNH 9.1.5.28) synonymized with *M. paululus* by Maeda (1982), *M. blepotis* (BMNH 9.1.5.444–59) and *M. macrodens* (BMNH 9.1.5.460–1). It



Figs 41–46 *Calcarmyobia mollis* sp. n.: holotype male (41); genital shield of male (42); modified claw on leg II of male (43); modified seta on genu II of male (44); allotype female (45); genito-anal setae of female (46).

is not so difficult to postulate that all above *Miniopterus* had been lumped together in a container somewhere before being separated again in the BMNH. *C. miniopteris* and *C. australasiae* are known as specific parasites of *M. macrodens* and *M. paululus,* respectively (Uchikawa, 1982), and are thought to have been transferred from the true hosts to the above *M. medius.* Then, *M. medius* and /or *M. blepotis* must be the host or hosts of *C. hamata longisetae.* As the Bornean *M. blepotis* (det. Maeda) is the type host of *C. hamata hamata,* the Javanese *M. blepotis* may likewise be the true host of *C. hamata longisetae.* Similarly the Bornean *blepotis* is different from the *blepotis* from Java, the type locality of *M. blepotis,* and has its own subspecies of the mite. Although it is possible for *M. medius* and *M. blepotis* to share a mite, as seen in some examples of the different bats (Uchikawa, 1982), both the bats could have respective mites. A Malaysian bat labelled *M. medius* in the FMNH (64169–74) yielded a new mite of the same genus as described later. If its host is reconfirmed as being *M. medius,* the mite may be a true parasite of *M. medius.*

Calcarmyobia mollis sp. n.

MALE (Figs 41, 42, 43 & 44). Slightly small sized species. Seta *vi* not inflated posteriorly. Structure of genital shield resembling those of *C. hamata* sspp., but *gp* membranous. Setae d_1 and d_2 stout. Modified claw on leg II forked and subequal in size to normal one. Modified seta on genu II not so strong.

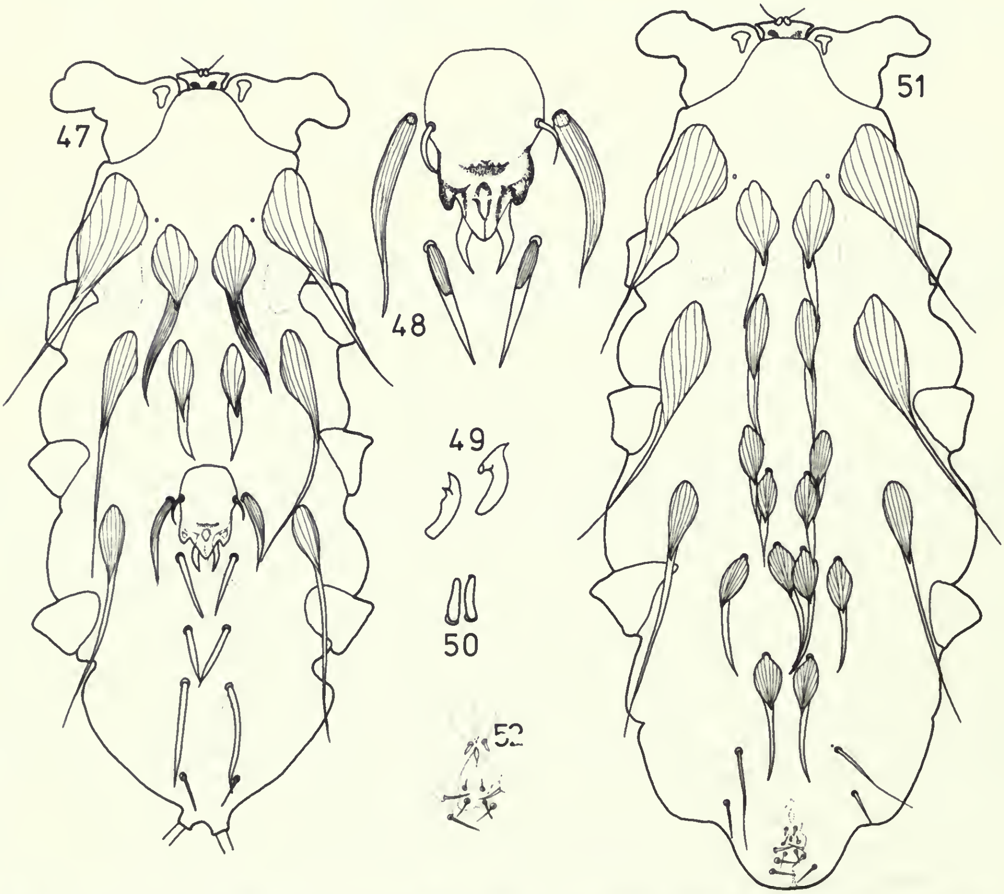
Measurements in µm for holotype and a paratype followed by those for 2 paratypes in paranetheses. Body 420–415 (430–440) long by 180–175 (190–210) wide. Seta *ve* 141–145 (155–140); *vi* 117–118 (120–113); *sc e* 160–155 (165–138); *sc i* 70–68 (68–65); d_1 40–40 (35–40); d_2 55–50 (55–53); d_3 45–43 (43–40); l_1 140–145 (148–135); l_2 68–65 (80–65). Genital shield 45–45 (43–47) long; *ga–ga* 33–30 (32–33). Modified seta on genu II 17–17 (15–18).

FEMALE (Figs 45 & 46). Seta d_1 with short tail; d_1 situated slightly anterior to basal level of l_2. A pair of small scales dorso-laterally on opisthosoma. Anal seta *ai* clavete.

Measurements in µm for allotype and 2 paratypes. Body 550 (555–550) long by 235 (235–250) wide. Seta *ve* 157 (?–158); *vi* 110 (105–120); d_1 53 (60–58); d_2 73 (75–70); d_3 98 (88–90); d_4 83 (90–90); l_1 185 (183–175); l_2 83 (88–85); d_1–d_1 47 (50–55); d_2–d_2 25 (25–24); d_3–d_3 18 (15–20); l_2–l_2 65 (60–68).

MATERIAL EXAMINED. Holotype male, allotype female and a paratype male ex *Miniopterus* (labelled *medius*), Palopo, Wawondula, S. Sulawesi, IX–1972 (USNM 501664–9); 2♂♂1♀ ex *M. pusillus pusillus*, Lequi-Mai, E. Timor, 22/23-IV-1968 (AMNH 237834–61); 1♀ ex *Miniopterus* (labelled *australis*), Atsabe, E. Timor (AMNH 237828).

REMARKS. *Calcarmyobia mollis* sp. n. and *C. hamata* sspp. are very close to each other in having almost identical genital shields in the male. The former is, however, smaller than the latter, and bears a forked claw on leg II, while the corresponding claw is hooked in the latter.



Figs 47–52 *Calcarmyobia mirabilis mirabilis* sp. n., ssp. n.: holotype male (47); genital shield of male (48); modified claw on leg II of male (49); modified seta on genu II of male (50); allotype female (51); genito-anal setae of female (51).

Although the host records of *C. mollis* are given above, complicated problems are inherent to the taxonomy of the bats judging from parasitological data obtained so far. The Thai bat formerly named *M. australis*, and revised as *M. pusillus* by Maeda (1982), is one of the hosts of *C. australasiae* Fain et Lukoschus (Uchikawa *et al.*, 1983), while the bat named *M. pusillus pusillus* from E. Timor yielded *C. mollis*. Thus, Maeda's definition of *M. pusillus* and that curated in the AMNH seems to be different from each other. Also *M. australis* is not the true host for the new species from Timor. Similar comments may be applied to *M. medius*.

Calcarmyobia mirabilis mirabilis sp. n., ssp. n.

MALE (Figs 47, 48, 49 & 50). Setae *vi* tapering; d_1 situated at level of *ga*, distinctly stronger than d_2. Genital shield as in Fig. 48; *ga* stout; *gp* sharply pointed and pincer-like. Modified claw on leg II forked and smaller than normal one; modified seta on genu II small.

Measurements in µm for holotype and a paratype. Body 470–470 long by 200–200 wide. Seta *ve* 158–153; *vi* 107–110; *sc e* 153–150; *sc i* 72–69; d_1 63–65; d_2 40–43; d_3 ?–48; l_1 145–158; l_3 65–78. Genital shield 63–63 long; *ga–ga* 33–33. Modified setae on genu II 12–13.

FEMALE (Figs 51 & 52). Hysterosomal submedian setae each with well developed striated part; d_3 situated slightly anterior to or almost on basal level of l_2. Genital setae g_7 slightly thicker than g_5; *ai* weakly inflated.

Measurements in µm for allotype and a paratype. Body 590–565 long by 260–260 wide. Seta *ve* 160–163; *vi* 103–102; *sc e* 178–180; *sc i* 108–110; d_1 63–65; d_2 65–70; d_3 88–75; d_4 88–85; l_1 190–175, l_2 78–73; d_1–d_1 48–50; d_2–d_2 25–25; d_3–d_1 20–18; l_2–l_2 65–68.

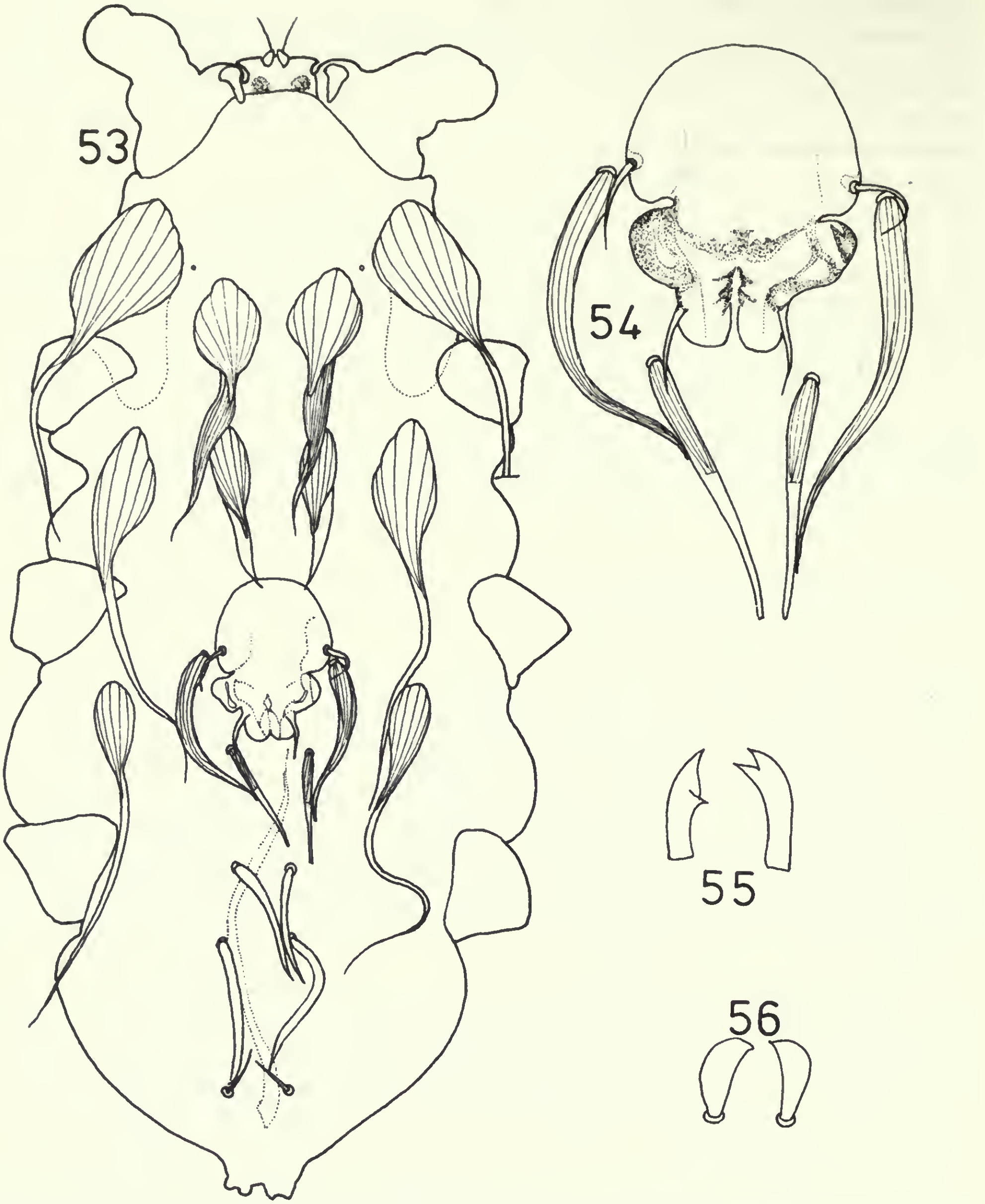
MATERIAL EXAMINED. Holotype male and allotype female ex *Miniopterus propitristis insularis*, New Guinea, Louisiades; Narian Misima Is., 8–XIII–1956 (AMNH 190479–82,–84–7); a pair of male and female paratypes from the same host, Terr. Papua: Kiriwina Is., 15–XII–1956 (AMNH 190733–6); 1♀ ex *M. propitristis propitristis,* Terr. Papua: Umi River, Markham River Valley, Morobe Dist., Papua New Guinea, 27–XI–1959 (AMNH 91401, Type); 1♂3♀♀ ex *M. propitristis*, Papua, West Division, Javareri, 10–II–1937 (AMNH 108507–16); ♀ ex *M. propitristis,* Terr. New Guinea: Kossam, Kratke Mts., 30–X–1959 (AMNH 191400); 2♂♂4♀♀ ex *M. propitristis,* Terr. New Guinea: Cape Vogel Peninsula, 16–IV–1953 (AMNH 157469); 3♂♂1♀ (1984.6.12.120–123) ex *Miniopterus*, 6 km inland from Wainoni Bay, San Christobal Is., Solomon (BMNH collector's number 316–7); 1♀ (1984.6.12.117) ex *M. tristis,* Espiritu Santo Is., New Hebrides (BMNH 36.4.8.3); 1♀ (1984.6.12.118) ex *M. tristis,* Hog Harbour, Espiritu Santo Is., New Hebrides (BMNH 73.1547–52); 1♂ (1984.6.12.119) ex *M. tristis,* Espiritu Santo Is., New Hebrides (BMNH 36.3.18.11).

REMARKS. The male of *C. mirabilis mirabilis* sp. n. is distinct in having the stout setae d_1, which are situated very close to *ga* and distinctly longer than d_2. The structure of the male genital shield is also quite different from those of the other known species in having small posterior lobes and forceps-like *gp*. Despite these remarkable specific characteristics in the male, the female is similar to those lacking opisthosomal scales. Thus it is virtually impossible to identify the mite, based only on female specimens.

The host bats of *C. mirabilis mirabilis* are *M. propitristis* sspp. and *Miniopterus* from the New Hebrides. *M. propitristis* was elevated to a full species in the *tristis* group (Peterson, 1981). *M. propitristis propitristis* and *M. propitristis insularis*, the hosts of *C. mirabilis*, are regarded as being different from *M. tristis* sspp. that harbour *C. brevis grandis* distinctly beyond the species level, thus supporting the treatment by Peterson (1981). *Miniopterus* from New Hebrides and the Solomon Islands are thought to be *M. propitristis* ssp., though some of them were identified as *tristis*.

Calcarmyobia mirabilis exilisetae ssp. n.

MALE (Figs 53, 54, 55 & 56). Genital shield with costal formation surrounded by a strong sclerite; width at level of costal formation almost the same as maximum width of shield slightly anterior to *ga*; posterior lobes broad and membranous ; *gp* thin. Seta d_1 slightly slenderer and longer than that of the nominate form. Modified seta on genu II inflated. Other morphological properties as in the nominate form.



Figs 53–56 *Calcarmyobia mirabilis exilisetae* ssp. n.: holotype male (53); genital shield of male (54); modified claw on leg II (55); modified seta on genu II of male (56).

Measurements in µm for holotype and, in parentheses, for 2 paratypes. Body 450 (455–460) long by 210 (210–215) wide. Setae *ve* 148 (153–?); *vi* 110 (108–108); *sc e* 155 (150–160); *sc i* 67 (65–65); d_1 ca. 70 (70–68); d_2 45 (55–47); d_3 50 (48–50); l_1 150 (140–?); l_3 ? (63–63). Genital shield 60 (62–62); *ga–ga* 38 (37–40). Modified seta on genu I 13 (13–13).

FEMALE. Unknown.

MATERIAL EXAMINED. Holotype male ex *Miniopterus,* Morobe Dist., Terr. New Guinea, 24–VII–1967 (BPSM 51234); 2 paratype males ex *Miniopterus* (labelled *tibialis*), Kaindi, Terr. New Guinea, 21–V–1959 (AMNH 191373–5, –7–80).

REMARKS. *Calcarmobia mirabilis exilisetae* ssp. n. is known only from the male. The genital shield is considerably different from that of the nominate form. The modified seta on genu II is inflated on all the specimens and quite different from that of the nominate form. The outline of the seta is, however, variable according to the state of mounted specimens.

The hosts of the mite, though it is recorded as *M. tibialis* above, are not determined, since *M. tibialis* is a probable host of *C. australasiae* as recorded below.

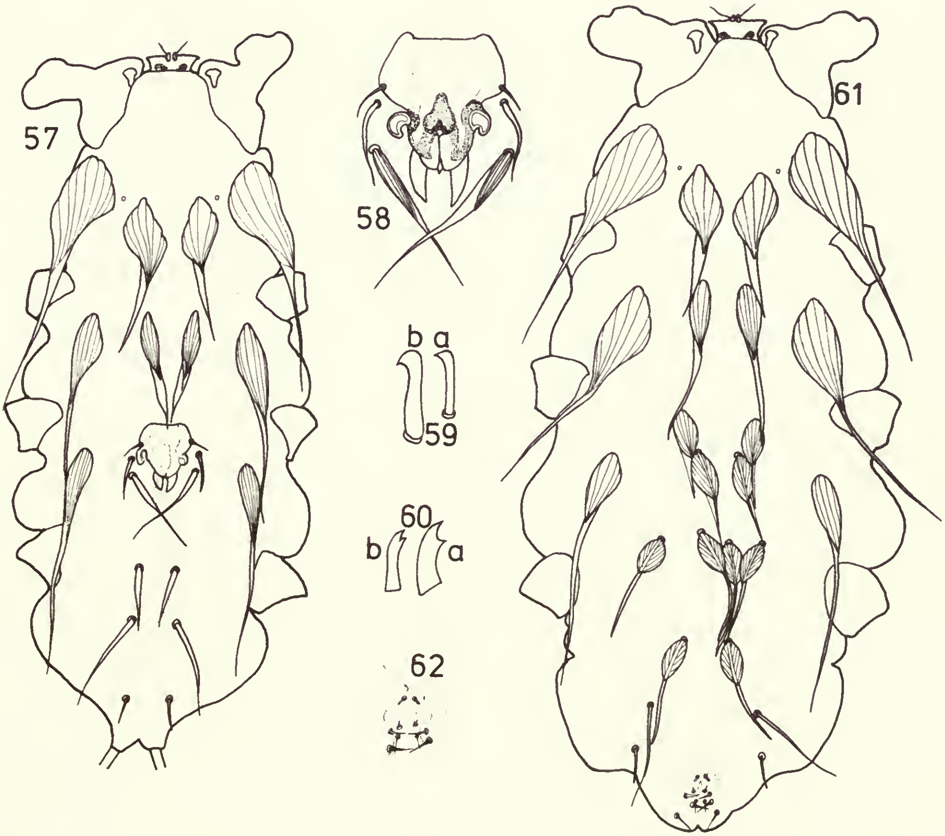
Calcarmyobia isosetae sp. n.

MALE (Figs 57, 58, 59 & 60). Small sized species. Seta *vi* the same in structure to that of the female. Genital shield similar to that of *C. australasiae; ga* fine; *gp* well developed. Seta d_2 fine posteriorly. Modified claw on leg II forked and stout; modified seta on genu II slender.

Measurements in µm for holotype. Body 430 long by 190 wide. Seta *ve* 155; *vi* 90; *sc e* ca. 130; *sc i* 70; d_1 ca. 28; d_2 55; d_3 40; l_1 ca. 150; l_3 63. Genital shield 45 long; *ga–ga* 35. Modified seta on genu II 15.

FEMALE (Figs 61 & 62). Seta d_1 with striated base and tail of almost the same length; basal striated part of d_2–d_4 and l_2 bulbous; d_3 closer to each other than to l_2. Genital seta g_5 wider at base and more prominent than g_7; *ai* swollen.

Measurements in µm for allotype. Body 550 long by 260 wide. Seta *ve* 173; *vi* 105; *sc e* 170; *sc i* 105; d_1 65; d_2 72; d_3 80; d_4 83; l_1 178; l_2 72; d_1–d_1 43; d_2–d_2 25; d_3–d_3 18; l_2–l_2 68.



Figs 57–62 *Calcarmyobia isosetae* sp. n.: holotype male (57); genital shield of male (58); modified seta on genu II of male (59a); modified claw on leg II of male (60a); allotype female (61); genito-anal setae of female (62). *Calcarmyobia australasiae* Fain & Lukoschus: modified seta on genu II (59b); modified claw of leg II of male (60b).

Table 1 List of hosts and localities of the mites of the genus *Calcarmyobia* Radford from the Oriental and Australasian regions dealt with in the present paper

Mite species	BMNH Accession Number	Host species	Locality	Code No.	Host Accession Number
*C. orianae orianae**		*M. orianae*	Darwin, Australia	42,68	USNM 284209–34
		M. (orianae)	Queensland, Australia	54	FMNH 60858
		M. (blepotis)	Queensland, Australia	57	FMNH 44245–7
		M. (schreibersi)	Misima Is., Papua	107	AMNH 190473–8
		M. (tibialis)	Morobe Dist., Papua	20	AMNH 195333–45
		M. (magnater)	Netherlands New Guinea	25	BSPM 21608
		M. (magnater)	Morobe Dist., Papua	184	BSPM 145400–3
*C. orianae eminens**	1984.6.12.114–115	*M. (schreibersi)*	Ceylon	102	BMNH 13.2.10.34–7
*C. biloba**		*M. macrocneme*	New Caledonia	1	BALM 1761,–63–6**
		M. macrocneme	New Caledonia	59	FMNH 55291–321
*C. brevis brevis**		*M. (australis pusillus)*	India	60	SMF 47841
*C. brevis grandis**		*M. tristis tristis*	Philippines	—	ROM 43655, 39860,–68
		M. tristis cerebensis	S. Sulawesi	15,51	AMNH 241557**–8
*C. brevis intermedia**		*M. eschscholtzii*	Philippines	55	FMNH 80384–431
		M. eschscholtzii	Philippines	82	USNM 17906
C. hamata hamata		*M. (blepotis)*	Sabah, Borneo	—	Uchikawa (1982)
*C. hamata breviungulae**		*M. haradai*	Thailand	—	—
*C. hamata longisetae**		*Miniopterus* sp.	W. Java	86	USNM 501673–87
		M. (schreibersi)	W. Java	64	USNM 501671
	1984.6.12.116	*M. (medius)*	S. Java	164	BMNH 9.1.5.462–3, 5–6
*C. mollis**		*M. (medius)*	S. Sulawesi	63	USNM 501664–9
		M. (pusillus pusillus)	E. Timor	103	AMNH 237834–61
		M. (australis)	E. Timor	104	AMNH 23728
*C. mirabilis mirabilis**		*M. propitristis insularis*	Misima Is., Papua	16	AMNH 190479–82, –84–7
		M. propitristis insularis	Kiriwina Is., Papua	17	AMNH 190733–6
		M. propitristis propitristis	Umi River, Papua	52	AMNH 91401**
		M. propitristis	W. Division, Papua	129	AMNH 10850–16
		M. propitristis	Kratke Mts., New Guinea	131	AMNH 191400
		M. propitristis	Terr. New Guinea	132	AMNH 157469
	1984.6.12.117	*M. (tristis)*	Espiritu Santo Is., New Hebrides	124	BMNH 36.4.8.3
	1984.6.12.118	*M. (tristis)*	Espiritu Santo Is., New Hebrides	126	BMNH 73.1547–52
	1984.6.12.119	*M. (tristis)*	Espiritu Santo Is., New Hebrides	127	BMNH 36.3.18–11
	1984.6.12.120–123	*Miniopterus*	San Christobal Is., Solomon Is.	32	BMNH 316–7 (Collector's number)
*C. mirabilis exilisetae**		*Miniopterus*	Morobe Dist., Papua	2	BSPM 51234
		M. (tibialis)	Kaindi, Terr. New Guinea	126	AMNH 191373–5, –7–80
*C. isosetae**		*M. (medius)*	Malaysia	52	FMNH 64169–74
C. australasiae		*M. (schreibersi)*	Misima Is., Papua	107	AMNH 190473–8
		M. australis	New Caledonia	154	BSPM 145549
		M. tibialis	Netherlands New Guinea	123	AMNH 152447–8
		M. tibialis	Kaindi, Terr. New Guinea	127	AMNH 191376
		M. tibialis	Lae, Terr. New Guinea	128	AMNH 191368–72
		M. tibialis	Papua	109	AMNH 158687–736
		M. tibialis	Queensland, Australia	21	AMNH 162684–701

Table 1 (Continued)

Mite species	BMNH Accession Number	Host species	Locality	Code No.	Host Accession Number
	1984.6.12.124	*M. tibialis*	Amboine	163	BMNH 7.1.1.557**
		M. (macrocneme)	New Georgia Is., Solomon Is.	58	FMNH 54808–42
		M. (macrodens)	Hong Kong	22	BSPM 65040
	1984.6.12.125	*M. (medius)*	Mountain Dist., New Guinea	77	BMNH 1938.8.3.34–6
	1984.6.12.126–127	*M. (medius)*	S. Java	164	BMNH 9.1.5.462–3, –5–6

*New taxon of the mites. **Type specimen(s) of the bats. Specific names of the host bats in parentheses are to be reconfirmed.

MATERIAL EXAMINED. Holotype male and allotype female ex *Miniopterus* (labelled *medius*), Malaysia (FMNH 64169–74).

REMARKS. All the males of the known species of the genus *Calcarmyobia* bear the seta *vi* quite different in form and nature from the homologous seta of their respective females. Thus, *Calcarmyobia isosetae* sp. n. is remarkable in having the seta essentially the same in both the sexes.

C. isosetae is allied to *C. australasiae* Fain & Lukoschus since both species have the male genital shields of almost the same structure. The genital seta *gp* is, however, stronger in *C. isosetate* than in *C. australasiae*. The modified seta on genu II and modified claw on leg II are also different in size in the two species as shown in Figs 59 and 60.

The females of *C. isosetae* and *C. australasiae* are barely separable from each other by the distance between the setae d_1, that is 43 µm in the former and 65 µm in the latter.

The holotype male and allotype female were taken from bats labelled *M. medius* in the FMNH, suggesting a complicated status of the taxonomy of the bats so named. If the host bats are really *medius*, the present new species is its specific parasite that suggests a close affinity of the bat to *M. australis*. In passing, *Pteracarus faini* Uchikawa was also found from the same bat specimens. This mite is known to occur on *M. fuliginosus, M. australis, M. pusillus* (det. by Maeda) and others (Uchikawa, 1985*b*).

Calcarmyobia australasiae Fain & Lukoschus, 1981

Calcarmyobia australasiae Fain & Lukoschus, 1981, *Bull. Ann. Soc. r. belge Ent.*, **116:** 46; Uchikawa, 1982, *Annot. zool. Japon.*, **55:** 35; Uchikawa *et al.*, 1983, *Acarologia*, **24:** 180. *Calcarmyobia miniopteris* (Womersley, 1941), Fain & Lukoschus, 1979, *Rec. West. Aust. Mus.*, **7:** 92.
Calcarmyobia sp., Uchikawa *et al.*, 1980, *Contr. biol. Lab. Kyoto Univ.*, **26:** 111.

MATERIAL EXAMINED. One ♀ ex *Miniopterus* (labelled *schreibersi*), Misima Is., Papua New Guinea, 8–XIII–1956 (AMNH 190473–8); 1♂ ex *M. australis*, New Caledonia, 30–III–1969 (BSPM 145549); 4♂♂1♀ ex *M. tibialis*, Netherlands New Guinea, 14–I–1939 (AMNH 152447–8); 1♂ 2♀♀ ex *M. tibialis*, Kaindi, Terr. New Guinea, 21–V–1959 (AMNH 191376); 3♂♂3♀♀ ex *M. tibialis*, Lae, Terr. New Guinea, 30–III–1959 (AMNH 191368–72); 3♂♂2♀♀ ex *M. tibialis*, Queensland, Australia, 15–II–1948 (AMNH 162684–701); 1♂ (1984.6.12.124) ex *M. tibialis*, Amboine (BMNH 7.1.1.557, Type); 2♀♀ ex *M. macrocneme*, New Georgia Is., Solomon Islands, 17–X–1943 (FMNH 54808–42); 1♂ ex *M. macrodens*, Hong Kong, 18–XIII–1964 (BSPM 65040); 1♂ (1984.6.12.125) ex *M. medius*, Mountain Dist., New Guinea (BMNH 1938.8.3.34–6); 1♂1♀ (1984.6.12.126–127) ex *M. medius*, Kalipoetjang, Tjitandoei River, S. Java, 4–IV–1908 (BMNH 9.1.5.462–3, –5–6).

REMARKS. The type host of *C. australasiae* Fain et Lukoschus is *M. australis* from Western Australia. A male was found on the type of *M. tibialis* (BMNH 7.1.1.557) in the present study.

A list of the hosts and localities of all the mites dealt with in the present paper is given in Table 1. The host species in parentheses are to be re-examined further taxonomically.

Acknowledgements

Gratitude is expressed to the curators and other staffs of the Mammal Section of all the Museums listed above for allowing the author to examine the bats deposited in their collections for ectoparasites. Thanks are also due to Mr K. H. Hyatt, British Museum (Natural History), for critical reading of the manuscript.

References

Fain, Alex & Lukoschus, S. F. 1979. Parasites of Western Australia. VI. Myobiidae parasitic on bats (Acarina: Prostigmata). *Rec. West. Aust. Mus.*, **7:** 61–107.

—— & —— 1980. Notes on the genus *Calcarmyobia* Radford, 1948 (Acari, Myobiidae). *Bull. Ann. Soc. r. belge. Ent.*, **116:** 45–47.

Hill, John Edwards & Jeffrey A. McNeely. 1975. The bats and bats' parasites of Thailand. U.S. Army Research & Development Group Far East Report Number FE-516-1 (Final Report). 87 pp.

Maeda, Kishio 1982. Studies on the classification of *Miniopterus* in Eurasia, Australia and Melanesia. *Honyurui Kagaku* (*Mammal Sci.), Suppl.* No. 1: 1–176.

Peterson, Randolph L. 1981. Systematic variation in the *tristis* group of the bent-winged bats of the *genus Minopterus* (Chiroptera: Vespertilionidae). *Can. J. Zool.*, **59:** 823–843.

Uchikawa, Kimito 1982. Mites of the genera *Calcarmyobia* and *Pteracarus* (Trombidiformes, Myobiidae) parasitic on *Miniopterus* (Chiriptera). *Annot. zool. Japon.*, **55:** 32–45.

—— 1985*a*. Mites of the genus *Calcarmyobia* (Acarina, Myobiidae) with information on the taxonomy of their host bats of the genus *Miniopterus* (Chiroptera, Miniopteridae). *Bull. Br. Mus. nat. Hist. (Zool.)*, **48:** 15–25.

—— 1985*b*. Mites of the genus *Pteracarus* (Acarina, Myobiidae) taken from the bats of the genus *Miniopterus* (Chiroptera, Miniopteridae). *Zool. Sci.*, **2.** In press.

Uchikawa, Kimito, Kishio Maeda, Masashi Harada & Tsuneaki Kobayashi 1980. Bat Myobiidae from Sabah, Borneo. *Contr. Biol. lab. Kyoto Univ.*, **26:** 97–121.

Uchikawa, Kimito, Masashi Harada, Songskadi Yenbutra & Sugishi Ohtani 1983. Bat Myobiidae from Thailand (Acarina, Trombidiformes). *Acarologia* **24:** 179–180.

Manuscript accepted for publication 4 July 1984

Calcarmyobia from the Ethiopian region (Acarina, Myobiidae)*

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Introduction

The author has sought to locate as many species and specimens of bats of the genus *Miniopterus* from the Ethiopian region as possible in the collections of the big museums in the United States and Europe for mites of the genus *Calcarmyobia*. All the four known species of the mites from the region were again recorded in the present study (Uchikawa, 1985*b*), and the five new species or subspecies were also found as described below.

All the specimens dealt with in the present paper will be deposited in the collections of the American Museum of Natural History, New York (AMNH), the British Museum (Natural History), London (BMNH), the Museum National d'Histoire Naturelle, Paris (MNHN), Forschungs-Institut Senkenberg, Frankfurt (SMF) or the US National Museum (USNM), where they were collected.

The scales for Figures are the same to those in Figs 1–6.

As the present paper is the fourth and last report on the mites of the family Myobiidae taken from the bats of the genus *Miniopterus* in the big museums, a summary of the mites themselves and, adopting them as indicators, problems in host systematics will be made in discussion.

Calcarmyobia comoresensis Uchikawa

Calcarmyobia comoresensis Uchikawa, 1982, *Annot. zool. Japan.*, **55**: 39.

Calcarmyobia comoresensis Uchikawa was originally described as a parasite of *Miniopterus manavi* from the Comores Islands (Uchikawa, 1982). It is shown in the present study that the mite is also found in Madagascar. The type of *M. manavi* (BMNH 97.9.1.37) also yielded a female of this species. The anonymous mites in Uchikawa (1982) were identified as *C. comoresensis* in the present study.

MATERIAL EXAMINED. One ♂ and 1♀ (1984.6.12.128–129) ex *Miniopterus majori*, Vobima, Madagascar (BMNH 0.5.5.48); 1♀ (1984.6.12.130) ex *M. majori*, Bersroha, Madagascar (BMNH 32.7.19.1–2); ♂1♀ (1984.6.12.132–133) ex *M. scotinus*, Imasindrory, Madagascar (BMNH 97.9.1.41–3; 1♀ (1984.6.12.131) ex *M. manavi*, Imasindrory, Madagascar (BMHN 97.9.1.37, type); 1♀ ex *Miniopterus*, Tananarive, Tsimbazaza, Madagascar, 1–III–1948 (MNHN); 1♂ ex *Miniopterus*, Grotte d'Andalambezo, Madagascar (MNHN); 1♂4♀♀ ex *M. scotinus*, Madagascar (MNHN 1912–44, *Calcarmyobia* sp. nr. *kenyaensis* in Uchikawa, 1982).

Calcarmyobia steatosetae steatosetae sp. n., ssp. n.

MALE (Figs 1, 2, 3 & 4). Seta *vi* thickened posteriorly, rather short and not reaching to genital shield. Seta d_1 distinctly thinner than d_2. Genital shield bearing *gp*, which is modified into a process. Modified claw on leg II only slightly inferior in thickness and length to normal one; modified seta on genu II as in Fig. 4; a thickened seta ventrally on tarsus II. Penis curved.

Measurements in µm for holotype and a paratype. Body (=gnathosoma+idiosoma) 460–460 long by 195–200 wide. Seta *ve* 138–142 long; *vi* 120–117 long; *sc e* ?–150 long; *sc i* 85–85 long; d_1 33–35 long; d_2 35–40 long; d_3 43–43 long; l_1 145–142 long; l_3 63–65 long. Genital shield 55–52 long (excluding *gp*); distance between *ga*, *ga–ga*, 37–35. Modified seta on genu II 20–21 long. Penis *ca.* 150–153 long.

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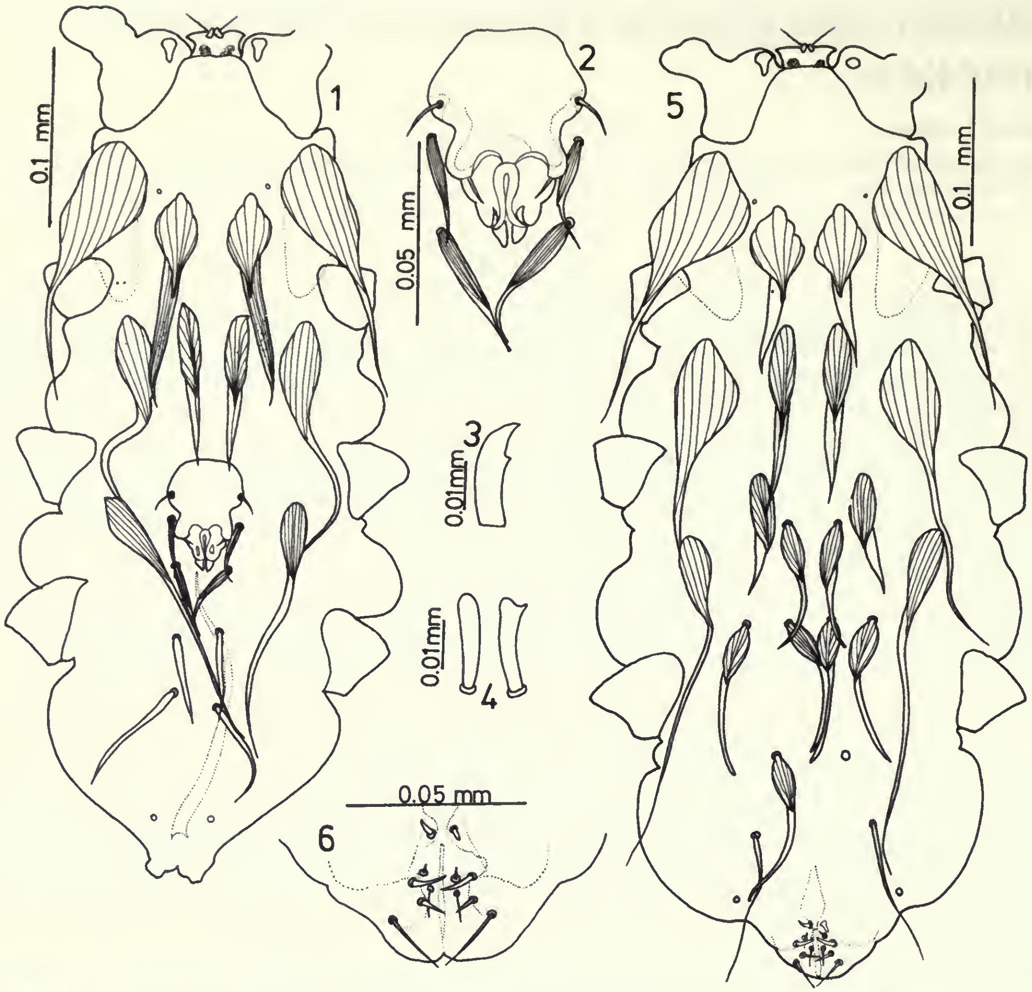
*Supported financially by Overseas Scientific Research Grant Nos 57041019 and 5803013 from the Ministry of Education, Science and Culture, Japan. Contribution No. Ac-4.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(1): 45–55 Issued 28 February 1985



Figs 1–6 *Calcarmyobia steatosetae steatosetae* sp. n., ssp. n.: holotype male (1); genital shield of male (2); modified claw on leg II of male (3); modified seta on genu II of male (4); allotype female (5); genito-anal setae of female (6).

FEMALE (Figs 5 & 6). Seta d_1 distinctly shorter than d_2; striated basal part of d_2 longer than tail; d_3 and l_2 originating from almost the same level. Anal seta *ai* clavate, smaller than that of *C. comoresensis;* g_7 stout and rather short; g_5 prominent.

Measurements in µm for allotype and, in parentheses, for 2 paratypes. Body 540 (570–550) long by 250 (?–250) wide. Seta *ve* 170(163–160); *vi* 102 (108–100); *sc e* 183 (198–195); *sc i* 108(110–110); d_1 70(63–66); d_2 80(75–72); d_3 90(90–85); d_4 95(85–88); l_1 198(193–*ca.* 200); l_2 90(85–83); d_1–d_1 60(60–62); d_2–d_2 30(30–25); d_3–d_3 23(20–22); l_2–l_2 72(78–72); d_4–d_4 40(35–30).

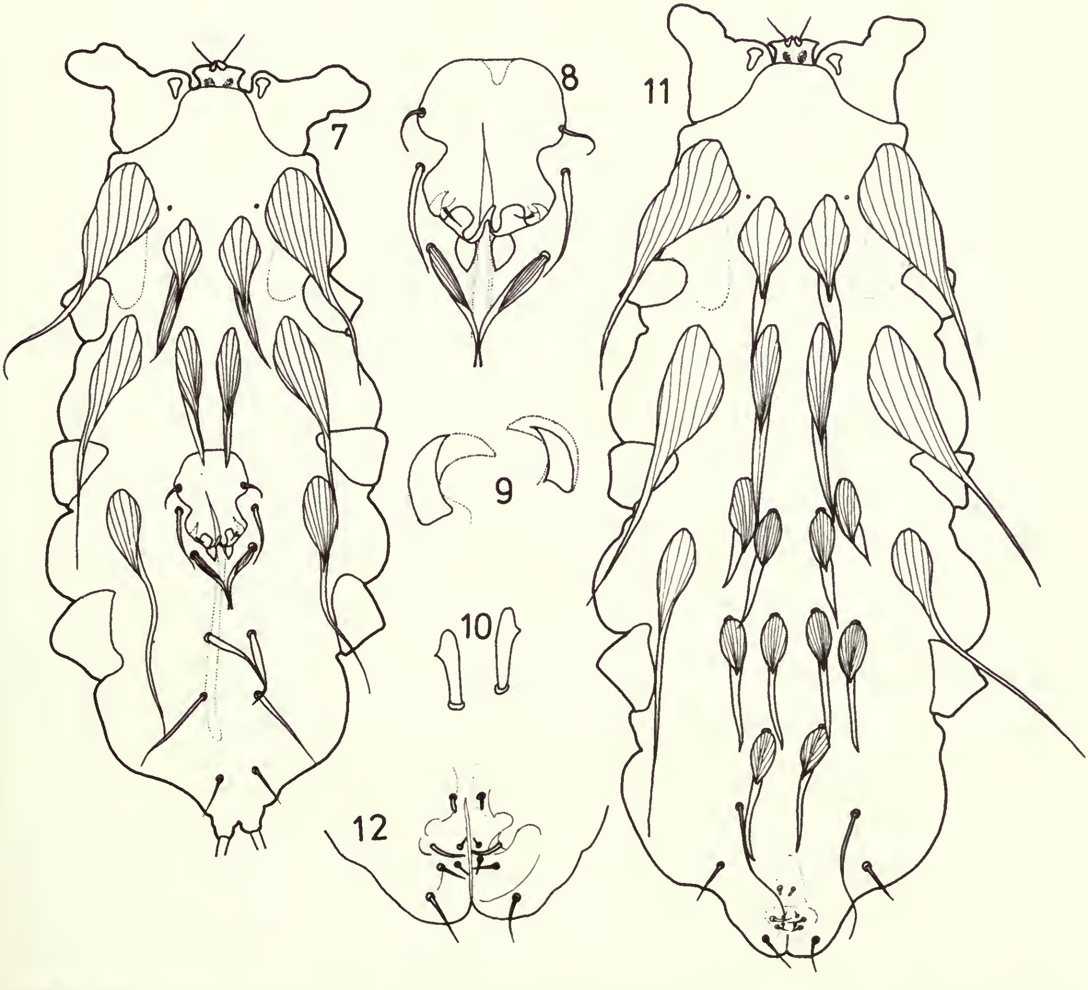
MATERIAL EXAMINED. Holotype male (1984.6.12.134) and allotype female (1984.6.12.135) ex *Miniopterus manavi*, Bealanana, N. Madagascar (BMNH 25.12.9.18–21); paratype male, 2 paratype females and 1♀ ex *Miniopterus*, Montague d'Ambre, Madagascar (MNHN; M–82 and others by Maeda); 1♂2♀♀ (1984.6.12.136–138) ex *M. manavi*, Nanavimenu, Madagascar (BMNH 77.2.19.1–5, 7); 1♀ (1984.6.12.139) ex *M. manavi*, Vinanitelo, Madagascar, 30–V–1896 (BMNH 97.9.1.40).

REMARKS. *Calcarmyobia steatosetae steatosetae* sp. n., ssp. n. resembles *C. comoresensis* Uchikawa, but is distinct in having seta *vi* short not reaching to the genital shield in the male. The posterior formation of the male genital shield is also quite different in the new species and in *C. comoresensis,* that is, *gp* is short and swollen in the former, while it is missing in the latter. The females of *C. steatosetae steatosetae* and *C. comoresensis* are barely separable from each other by the nature of the anal seta *ai* and genital seta g_7. The seta *ai* is distinctly smaller on *C. steatosetae steatosetae* than on *C. comorensis,* and g_7 of *C. steatosetae steatosetae* is slightly thicker and shorter than that of *C. comoresensis.*

The present new mite is recorded only from Madagascar, and its host is *M. manavi* subject to confirmation.

Calcarmyobia steatosetae rectipenis ssp. n.

MALE (Figs 7, 8, 9 & 10). Seta *vi* very short; its tail distinctly shorter that striated basal part. Genital shield deformed, but bearing swollen *gp.* Modified claw on leg II distinctly smaller than normal one, and probably simple in shape; modified seta on genu II rather long. Penis almost straight and short.



Figs 7–12 *Calcarmyobia steatosetae rectipenis* ssp. n.: holotype male (7); genital shield of male (8); modified claw on leg II of male (9); modified seta on genu II of male (10); allotype female (11); genito-anal setae of female (12).

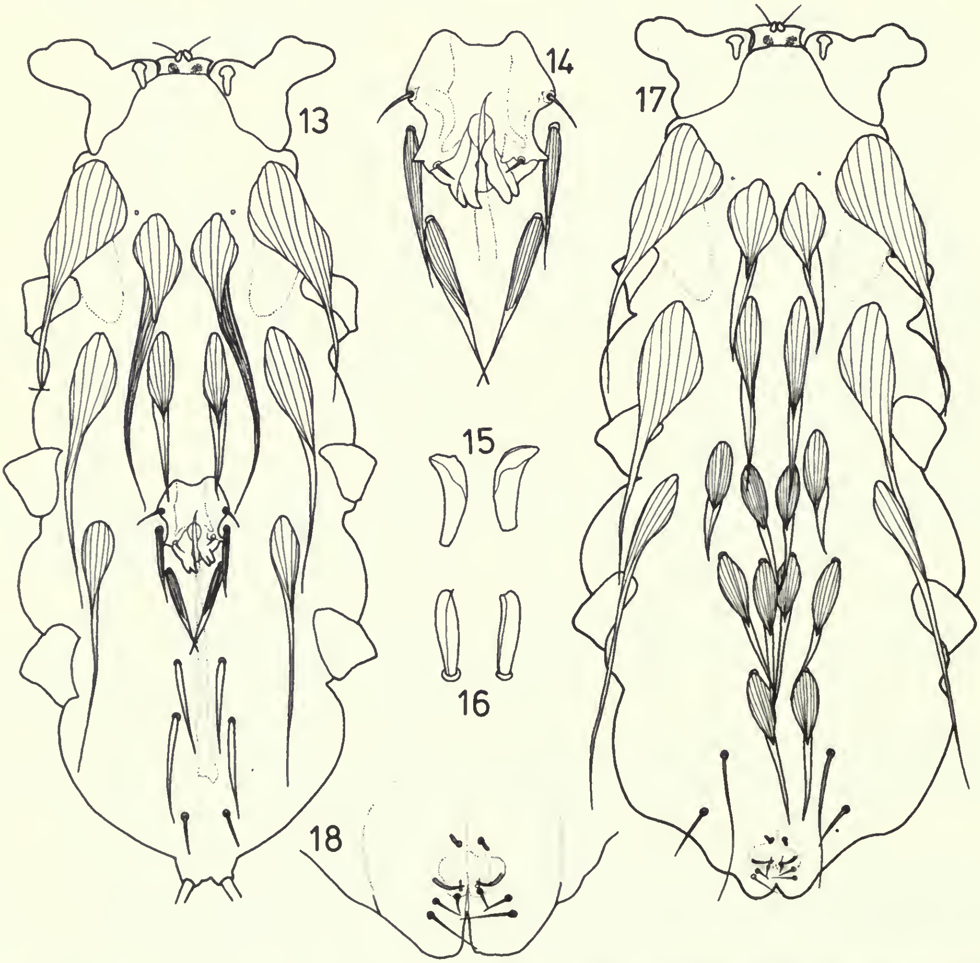
Measurements in µm for holotype. Body 410 long by 180 wide. Seta *vi* 84(striated part 53); *sc e* 125; *sc i* 79; d_1 *ca.* 35; d_2 38; d_3 *ca.* 42; l_1 *ca.* 133; l_3 53. Genital shield 52 long (excluding *gp*); *ga–ga* 35. Modified seta on genu II 23. Penis 133.

FEMALE (Figs 11 & 12). Setae d_1 and d_2 subequal in length; setae g_7 slenderer and g_5 and *ai* weaker than corresponding setae of nominate form. Other structures as in nominate form.

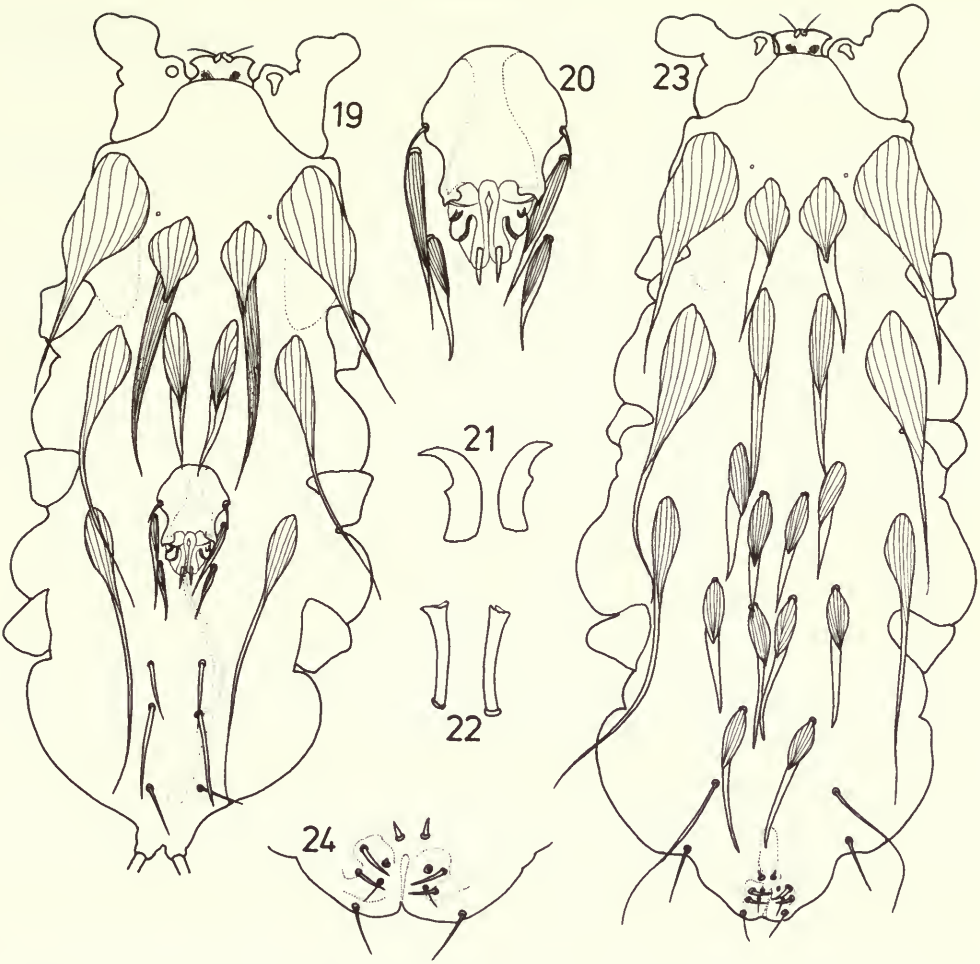
Measurements in µm for allotype. Body 540 long by 230 wide. Seta *ve ca.* 160; *vi* 100; *sc e* 163; *sc i* 115, d_1 65; d_2 66; d_3 80; d_4 82; l_1 *ca.* 185; l_2 75; d_1–d_1 58; d_2–d_2 27; d_3–d_3 23; l_2–l_2 70; l_4–l_4 30.

MATERIAL EXAMINED. Holotype male and allotype female ex *Miniopterus manavi*, Andrandoka (found in cave), Madagascar, 7–XII–1951 (USNM 294524–9).

REMARKS. Although the genital shield of the male, one of the most important properties for distinguishing the species of *Calcarmyobia*, is not clearly observed, the structure of the shield is essentially the same to that of *C. steatosetae steatosetae*. The measurement of setae *vi*, form of the modified claw on leg II and of the modified seta on genu II, are unique in the male of the present



Figs 13–18 *Calcarmyobia exserta* sp. n.: holotype male (13); genital shield of male (14); modified claw on leg II of male (15); modified seta on genu II of male (16); allotype female (17); genito-anal setae of female (18).



Figs 19–24 *Calcarmyobia minoris* sp. n.: holotype male (19); genital shield of male (20); modified claw on leg II of male (21); modified seta on genu II of male (22); allotype female (23); genito-anal setae of female (24).

form. Further, the relative length of d_1 and d_2 and the nature of *ai* and g_7 of the female are slightly different in both the present subspecies and the nominate form.

The host bats are again identified as *M. manavi,* but it is necessary to reconfirm their identity.

Calcarmyobia exserta sp. n.

MALE (Figs 13, 14, 15 & 16). Seta *vi* long, fully reaching to *ga*; d_1 and d_2 and similar; d_3 rather slenderer. Genital shield protruding laterally at level of *gm*. Modified claw on leg II as in Fig. 16; its lateral view not obtained. Modified seta on genu II short. Penis straight.

Measurements in µm for holotype. Body 440 long by 190 wide. Seta *ve* 135, *vi ca.* 165; *sc e* 150; *sc i* 85; d_1 38; d_2 50; d_3 47; l_1 150; l_3 58. Genital shield *ca.* 53 long; *ga–ga* 35. Modified seta on genu II 18. Penis 148.

FEMALE (Figs 17 & 18). Seta d_1 distinctly shorter than d_2; striated basal part of d_1 long (45–50 µm) and slender; striated basal part of d_2–d_4 and l_2 also slender; d_3 and l_2 originating from almost the same level. Anal seta *ai* clavate but not so prominent; g_5 weak.

Measurements in µm for allotype and 3 paratypes. Body 510 (530–550) long by 220(240–245) wide. Seta *ve* 158(155–160); *vi* 108 (95–105); *sc e* 188(182–188); *sc i* 118(120–120); d_1 72(67–78); d_2 80(75–83); d_3 88(88–95); d_4 90(85–90); l_1 >210(205–205); l_2 85(80–83); d_1–d_1 55(48–58); d_2–d_2 24(20–28); d_3–d_3 18(18–20); l_2–l_2 64(68–70); d_4–d_4 30(30–30).

MATERIAL EXAMINED. Holotype male, allotype female and 3 paratype females ex *Miniopterus*, Namoroka, Madagascar, IX-1952 (MNHN); 1♀ ex *Miniopterus*, Andalambezo, Madagascar, VII–1956 (MNHN); 1♀ ex *Miniopterus*, Ambohimirija, Madagascar, IX-1952 (MNHN).

REMARKS. The male of *Calcarmyobia exserta* sp. n. is distinct in having the genital shield with the lateral protuberance level with *gm*. Among the known species of the genus *Calcarmyobia*, *C. kenyaensis* Uchikawa also bears a similar protruberance. This species is, however, different from the present new species in having a pair of normal or unmodified claws on leg II.

The female of *C. exserta* is very close to those of the other two species, *C. comoresensis* and *C. steatosetae steatosetae*, distributed in Madagascar. *C. comoresensis* bearing strong *ai* is easily distinguished from the other two species; *C. steatosetae steatosetae* and the present new species are separable from each other by the combination of the nature of the setae d_1 and g_5. The striated basal part of d_1 is longer and slenderer and g_5 is finer in the former than in the latter.

Calcarmyobia minoris sp. n.

MALE (Figs 19, 20, 21 & 22). Seta *vi* rounded anteriorly, reaching to genital shield; d_1 distinctly longer and thicker than d_2; d_2 and d_3 situated widely apart from each other. Genital shield bearing fine and long *gm* and thickened and simple *gp*. Modified claw on leg II as in Fig. 21; modified seta on genu II long.

Measurements in µm for holotype and, in parentheses, for 2 paratypes. Body 430(470–480) long by 190(200–210) wide. Seta *ve ca.* 140(155–143); *vi* 150(150–155); *sc e* 170(170–170); *sc i* 82(83–84); $d_1$45(43–45); d_2 35(35–30); d_3 30(40–40); d_2–d_3 60(66–60); l_1 160(160–?). Genital shield 58(62–62) long; *ga–ga* 37(42–40). Modified seta on genu II 23(24–25). Penis *ca.* 150(150–145).

FEMALE (Figs 23 & 24). Seta d_1 almost the same in length to d_2; striated basal part and tail of d_1 subequal in length; d_3 originating from slightly or distinctly posterior to basal level of l_2; striated basal part of d_1–d_4 and l_2 rather slender and less than 15 µm. Anal seta *ai* weakly clavate; g_7 slightly thicker than g_5.

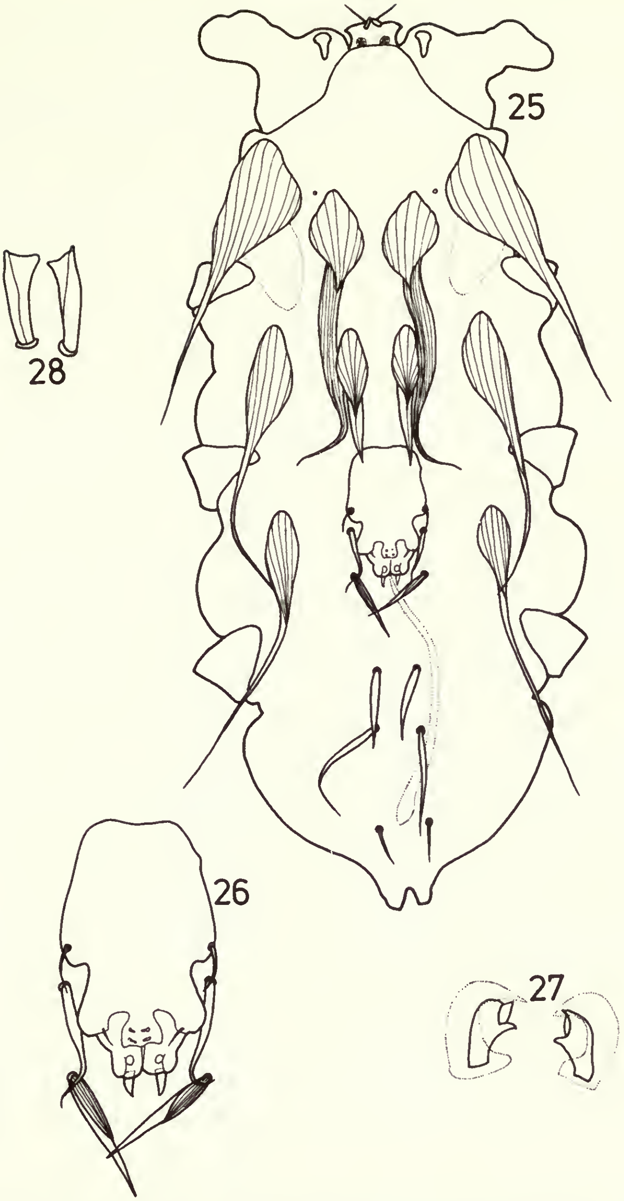
Measurements in µm for allotype and 2 paratypes. Body 525(540–550) long by 230(250–245) wide. Seta *ve* 163(170–163); *vi* 105(103–95); *sc e ca.* 200(?–195); *sc i* 110(115–108); d_1 73(78–75); d_2 70(78–80); d_3 80(88–88); d_4 78(83–90); l_1 213(220–225); l_2 75(78–88); d_1–d_1 57(60–55); d_2–d_2 24(23–24); d_3–d_3 20(20–22); l_2–l_2 65(65–62); d_4–d_4 38(33–31).

MATERIAL EXAMINED. Holotype male and allotype female ex *Miniopterus minor minor*, Similani Cave, 16 km S. of Mombasa, Coast Province, Kenya, 29–IX–1975 (AMNH 237341–3); a pair of male (1984.6.12.140) and female (1984.6.12.141) paratypes, 4♂♂(1984.6.12.142–145) and 4♀♀ (1984.6.12.146–148) ex *Miniopterus* sp., Shimoni, Mombasa, Kenya (BMNH 11.12.10.14–21); a pair of male (1984.6.12.149) and female (1984.6.12.150) paratypes, 2♂♂ (1984.6.12.151–152) and 2♀♀ (1984.6.12.153–154) ex *M. minor*, Amboni Caves, Tanga, Tanzania (BMNH 52.1333–63).

REMARKS. The male of *C. minoris* sp. n. is distinct in having d_1, which is distinctly thicker and longer than d_2, and the long and slender modified seta on genu II. The structure of the genital shield of the new species is almost the same as that of *C. congoensis* sspp., yet the length of the shield and the nature of *gp* are slightly different in both species.

The female of *C. minoris* is characterized by dorsal seta d_3 originating from the posterior level of the base of l_1.

The host bat is thought to be *Miniopterus minor*, and the distribution of the mite is so far restricted to the eastern coast of the central part of Africa.



Figs 25–28 *Calcarmyobia producta* sp. n.: holotype male (25); genital shield of male (26); modified claw on leg II of male (27); modified seta on genu II of male (28).

Calcarmyobia producta sp. n.

MALE. (Figs 25, 26, 27 & 28). Seta *vi* reaching to genital shield; striated basal part of *sc i* swollen, widest at middle; d_1 distinctly thinner than d_2. Genital shield long, especially with elongate anterior part; *gp* weakly inflated. One claw on leg II shorter than the other and strongly modified; modified seta on genu II thick and rather long. Penis curved.

Measurements in µm for holotype and, in parentheses, for 2 paratypes. Body 470(480–470) long by 210(205–210) wide. Seta *ve* ?(162–145); *vi* ?(160–153); *sc e* 160(?–160); *sc i* 78(75–75); d_1 43(38–38); d_2

45(35–39); d_3 51(43–47); l_1 ?(167–170); l_2 ?(60–75). Genital shield 70(68–69); *ga–ga* 40(40–40). Modified seta on genu II 22(20–22). Penis *ca.* 160(1558-*ca.* 150).

FEMALE. A female specimen was taken together with the holotype of the present new species from the type specimen of *Miniopterus schreibersi pulcher*. This specimen was not separable from the female of the atypical form of *C. congoensis,* and was not definitely identified as the partner female of *C. producta* sp. n.

MATERIAL EXAMINED. Holotype male (1984.6.12.155) (and a female 1984.6.12.156) ex *Miniopterus schreibersi pulcher,* Kurdistan, N. Iraq, 6–VIII–1954 (BMNH 67.1230, type); 2 paratype males ex *Miniopterus* (labelled *inflatus),* N. Chyulu Hills, Kenya, 7–V–1979 (SMF 57588).

REMARKS. The male of *C. producta* sp. n. is distinct in having the genital shield with elongate anterior part. The hosts of the new mite are listed above, but it is not clear whether they are true hosts or not.

A list of the hosts and localities of all the mites dealt with in the present paper is given in Table 1.

Table 1 List of hosts and localities of the mites of the genus *Calcarmyobia* Radford from the Ethiopian region dealt with in the present paper

Mite species	BMNH Accession Number	Host species	Locality	Code No.	Host Accession Number
C. comoresensis		*Miniopterus*	Madagascar	4	MNNH ——
		Miniopterus	Madagascar	6	MNHN ——
	1984.6.12.128–129	*M. majori*	Madagascar	180	BMNH 0.5.5.48
	1984.6.12.130	*M. majori*	Madagascar	181	BMNH 32.7.19.1–2
	1984.6.12.131	*M. manavi*	Madagascar	157	BMNH 97.9.1.37**
		M. scotinus	Madagascar	—	MNHN 1912–44
	1984.6.12.132–133	*M. scotinus*	Madagascar	56	BMNH 97.9.1.41–3
*C. steatosetae steatosetae**		*Miniopterus*	Madagascar	8	MNHN ——
	1984.6.12.134–135	*M. manavi*	Madagascar	179	BMNH 25.12.9.18–19
	1984.6.12.136–138	*M. manavi*	Madagascar	177	BMNH 77.2.19.1–5,7
	1984.6.12.139	*M. manavi*	Madagascar	178	BMNH 97.9.1.40
*C. steatosetae rectipenis**		*M. manavi*	Madagascar	61	USNM 294524–9
*C. exserta**		*Miniopterus*	Madagascar	11	MNHN ——
		Miniopterus	Madagascar	9	MNHN ——
		Miniopterus	Madagascar	10	MNHN ——
*C. minioris**	1984.6.12.140–148	*Miniopterus* sp.	Mombasa, Kenya	30	BMNH 11.12.10.14–21
		M. minor	Near Mombasa, Kenya	14	AMNH 237341–3
	1984.6.12.149–154	*M. minor*	Tanga, Tanzania	74	BMNH 52.1333–63
*C. producta**	1984.6.12.155 (–156)	*M. schreibersi pulcher*	N. Iraq	144	BMNH 67.1230**
		M. inflatus?	Kenya	43	SMF 57588

*New taxon, **Type specimen.

Discussion

The Ethiopian region mites, *Calcarmyobia rhinolophia* (Radford), the generic type, *C. congoensis* Uchikawa and *C. kenyaensis* Uchikawa, were described from continental Africa, and *C. comoresensis* Uchikawa from the Comores Islands (Uchikawa, 1982). All these species were obtained again in the present study as recorded in the previous paper (Uchikawa, 1985*b*), and 5 new

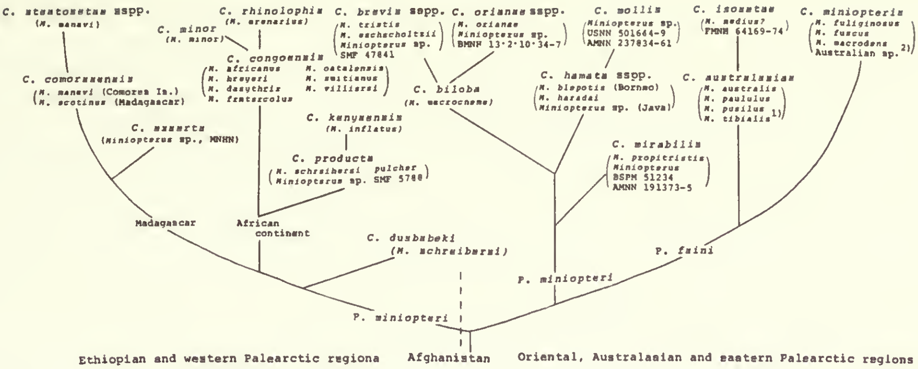

C. steatosetae sspp.
(M. manavi)
C. minor
(M. minor)
C. rhinolophia
(M. arenarius)
C. brevis sspp.
M. tristis
M. eschscholtzii
Miniopterus sp.
SMF 47841
C. orianae sspp.
M. orianae
Miniopterus sp.
BMNH 13·2·10·34-7
C. mollis
Miniopterus sp.
USNN 501664-9
AMNN 237834-61
C. isosetae
(M. medius?
FMNH 64169-74)
C. miniopteris
M. fuliginosus
M. fuscus
M. macrodens
Australian sp. 2)
C. comorasensis
M. manavi (Comores Is.)
M. scotinus (Madagascar)
C. congoensis
M. africanus
M. breyeri
M. dasythrix
M. fraterculus
M. natalensis
M. smitianus
M. villiersi
C. biloba
(M. macrocneme)
C. hamata sspp.
M. blepotis (Borneo)
M. haradai
Miniopterus sp. (Java)
C. australasiae
M. australis
M. paululus
M. pusilus
M. tibialis 1)
C. kenyaensis
(M. inflatus)
C. exserta
(Miniopterus sp., MNHN)
C. producta
M. schreibersi pulcher
Miniopterus sp. SMF 5788
C. mirabilis
M. propitristis
Miniopterus
BSPM 51234
AMNN 191373-5
Madagascar
African continent
C. dusbabeki
(M. schreibersi)
P. faini
P. miniopteri
P. miniopteri
Ethiopian and western Palearctic regiona
Afghanistan
Oriental, Australasian and eastern Palearctic regions

Fig. 29 Phylogenetic relationship among the mites of the genus *Calcarmyobia* parasitic on *Miniopterus* suggested by the formation of their male genital shields. Hosts of the mites are in parentheses. 1) Real *M. tibialis* is expected to harbour *P. faini*, 2) Species dealt with as *M. schreibersi* in Womersley (1941) and Fain & Lukoschus (1979).

species or subspecies were further added to the fauna in the present paper. Thus, the mites of the genus *Calcarmyobia* from the Ethiopian region come up at least to 9 species or subspecies. It is remarkable that no mite among the above 9 taxa occurs in both the continent and Madagascar. This might suggest that the bats of the genus *Miniopterus*, the specific hosts of *Calcarmyobia*, of both the subregions have become isolated from one another for a long time.

All the Ethiopian species of the mites, as well as *C. dusbabeki* Uchikawa distributed in the western Palearctic region, are thought to be closer to one another than to any of the mites from the Oriental, Australian and eastern Palearctic regions in having in common the male genital shields of a particular type which bears the genital seta *gm*. It should be noted that the shields of all the Oriental, Australasian and eastern Palearctic species lack the seta and bear the costal formation in place of the seta. As the genitalia of the mites are regarded as being conservative in evolution, the species with one type of genital shield are thought to be phylogenetically different from those with another type of shield. Thus, the mites from the Ethiopian and western Palearctic regions comprise a phylogenetic group that is separable from the other group consisting of the Oriental, Australasian and eastern Palaearctic species. This might be also the case for their host *Miniopterus*.

The distribution pattern of the mites of the genus *Pteracarus*, a very primitive myobiid genus parasitic on Vespertilionidae and their relatives, offers somewhat different information on their hosts. Only the 2 species, *P. miniopteri* Uchikawa and *P. faini* Uchikawa, have so far been known to occur on *Miniopterus*. It is proved that *P. miniopteri* is found on many kinds of the bats in almost the whole range of *Miniopterus* excluding the eastern Palearctic region, while *P. faini* is distributed on a few species of the bats in the Oriental, Australasian and eastern Palearctic regions. Accordingly, the host bats of these mites are regarded as being diphylogenetic, a host group for *P. miniopteri* and the other for *P. faini* (Uchikawa, 1985*a*). Contrary to the above deduction for mites of the genus *Calcarmyobia*, the host *Miniopterus* of *P. miniopteri* from all the Ethiopian, western Palearctic, Oriental and Australasian regions are regarded as being phylogenetically the same to one another, while the hosts of *P. faini* comprise the other group in the Oriental, Australasian and eastern Palearctic regions. These contradictory deductions might be synthesized as follows: The bats of the genus *Miniopterus* had been essentially monophylogenetic in origin, since such a conservative parasite as *P. miniopteri* is parasitic on so many kinds of the bats in almost the whole range of *Miniopterus*. Also, the bats of the Ethiopian and western Palearctic regions have been isolated for so long from those of the Oriental, Australasian and eastern Palearctic regions that the bats from either geographical range have their respective type of acarine parasites of the genus *Calcarmyobia*. As the host bats of *P. miniopteri* and *P. faini* harbour the same type of *Calcarmyobia* in the Oriental, Australasian and eastern Palearctic regions, the host group of *P. faini* is thought to be derived from the other group in a limited range in relatively recent times.

Miniopterus schreibersi, the generic type, had long been believed to occur in almost the whole range of *Miniopterus*, and thus many specimens of the bats from the Ethiopian, Oriental, Australasian and eastern Palearctic regions were identified as *M. schreibersi* or *M. schreibersi* sspp. in the collections of the big museums in Europe and the United States. *M. schreibersi* distributed in Romania, the type locality of the bat, and in other European countries is the host of *C. dusabeki*. This mite prevails in the western Palearctic region east to Afghanistan, and there meets *C. miniopteris* Womersley (Uchikawa, 1985*b*). In the other regions, different mites of the genus *Calcarmyobia* are found on the bats *M. schreibersi* or *M. schreibersi* sspp. As the mites of the genus are not synhospitalic, the bats that harbour different species of the mites could not be conspecific. Accordingly, it is reasonable to regard *M. schreibersi* as being distributed only in the range of *C. dusbabeki*, that is, the western Palearctic region (Uchikawa, 1985*b*). The bat of the genus *Miniopterus* distributed in the eastern Palearctic region from Afghanistan to the Far East, which harbours *C. miniopteris*, had long been considered as a subspecies of *M. schreibersi*. Although bats distributed in the same biogeographic range are ready to be regarded as being conspecific, the *Miniopterus* bats distributed in the western and eastern Palearctic regions are distinctly different from each other sufficiently beyond the subspecies level with a boundary around Afghanistan as elucidated above adopting acarine parasites as indicators. This might not be an exceptional case only for *Miniopterus*. Some bats of the other genera distributed in the different parts of the Palearctic region might have the same distribution pattern as that of *Miniopterus*.

The data for the mites of the genus *Calcarmyobia* are still fragmentary, and only the type specimens are known in some cases. On these records, it is still possible to postulate that the mites of this genus have rather limited distributional ranges. Even the 3 species of mites with the widest ranges do not prevail on the whole range of *Miniopterus*, and, in the Oriental region, closely related mites are often found on bats from islands near to each other (Uchikawa, 1985*c*). As different mites infest respective bats, this limited distribution pattern of the mites suggests the same pattern of their hosts. Because of their supposed movability, the Chiroptera have been excluded as a rule in the consideration in zoogeography. The distribution of some bats should, however, be regarded as being definite and limited from the data on the acarine parasites.

Myobiid mites serve as indicators in the taxonomy or phylogeny of their hosts (Uchikawa & Harada, 1981). Adopting the male genital shield of mites of the genus *Calcarmyobia* as the criterion, a scheme suggesting phylogenetic relationship among the mites is proposed as in Fig. 29. The records of *Pteracarus* are also included in the figure. These data might show the relationship among the host bats of the mites, which are also recorded in parentheses. The taxonomy of bats of the genus *Miniopterus* is still far from satisfactory and some ambiguous and/or incorrect specific names of the bats might have been adopted in the figure. The above parasitological deduction on the relationship among *Miniopterus* is contradictory in some points to the proposals recently made upon the improved methods by such chiropterologists as Peterson (1981) and Maeda (1982). The most striking difference between parasitological and anatomical deductions by Peterson (1981) and Maeda (1982) is that the bats of the *tristis* group are quite differently dealt with in Fig. 29. This suggests that the parasitological data are indicative of some phylogenetic aspects of host animals still unnoticed or unaccustomed in the traditional study of the host themselves. Further studies of both the parasites and their hosts are necessary to interpret such a problem.

Acknowledgements

Gratitude is expressed to the curators and other staffs of the Mammal Sections of all the Museums listed above for allowing the author to examine the bats deposited in their collections for ectoparasites. Thanks are also due to Mr K. H. Hyatt, British Museum (Natural History), for critical reading of the manuscript.

References

Fain, A. & Lukoschus, F. S. 1979. Parasites of Western Australia. VI. Myobiidae parasitic on bats (Acarina: Prostigmata). *Rec. West. Aust. Mus.*, **7:** 61–107.

Maeda, K. 1982. Studies on the classification of *Miniopterus* in Eurasia, Australia and Melaneasia. *Honyurui Kagaku (Mammal Sci.), suppl.* No. 1: 1–176.

Peterson, Randolph L. 1981. Systematic variation in the tristis group of the bent-winged bats of the genus *Miniopterus* (Chiroptera: Vespertilionidae). *Can. J. Zool.*, **59:** 823–843

Uchikawa, K. 1982. Mites of the genera *Calcarmyobia* and *Pteracarus* (Trombidiformes, Myobiidae) parasitic on *Miniopterus* (Chiroptera). *Annot. zool. Japon.*, **55:** 32–45.

—— 1985*a*. Mites of the genus *Pteracarus* (Acarin, Myobiidae) taken from the bats of the genus *Miniopterus* (Chiroptera, Miniopteridae). *Zool. Sci.* **2.** In press.

—— 1985*b*. Mites of the genus *Calcarmyobia* (Acarine, Myobiidae) with information on the taxonomy of their host bats of the genus *Miniopterus* (Chiroptera, Miniopteridae). *Bull. Br. Mus. nat. Hist.* (Zool.), **48:** 15–25.

—— 1985*c*. *Calcarmyobia* from the Oriental and Australasian regions. (Acarina, Myobiidae). *Ibid.*, **48:** 45–55.

—— **& Harada, M.** 1981. Evaluation of bat-infesting Myobiidae (Acarina, Trombidiformes) as indicators in taxonomy and phylogeny of host bats (Chiroptera). *Zool. Mag.*, **90:** 351–361.

Womersley, H. 1941. Notes on the Cheyletidae (Acarina, Trombidoidea) of Australia and New Zealand, with descriptions of new species. *Rec. S. Austral. Mus.*, **7:** 51–64.

Manuscript accepted for publication 4 July 1984

A revised synonymy of the minnow genus *Phoxinus* Rafinesque, 1820 (Teleostei: Cyprinidae) with comments on its relationships and distribution

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Introduction

Communication between scientists and the public will not be aided or enhanced by the overeager adoption of new names until the old ones have been shown to be inadequate. So comment Scott & Crossmann (1973) in response to the acceptance by some recent authors of Bănărescu's (1964) synonymy of the nearctic minnow genus *Chrosomus* with the palearctic *Phoxinus*. This particular case has highlighted the confusion of supra-specific cyprinid taxonomy and the fact that rigorous definitions of most cyprinid taxa just do not exist. Previous work has failed to make direct anatomical comparisons of the various genera and 'generic characters' have included morphometric and meristic variables such as body depth, number of lateral line scales, degree of completeness of the lateral-line, and peritoneal pigmentation. At best, such characters indicate specific, populational or individual differences. The inadequacy of such 'generic characters' is particularly evident when attempting to discriminate between so-called phoxinine genera; *i.e. Phoxinus, Phoxinellus* and *Pseudophoxinus* (see, for example, the remarks in Coad, 1981).

This review of the synonymy of *Phoxinus* has been initiated through a wider study embracing the phyletic classification of all Old-World leuciscine cyprinids. In the course of renewed efforts to identify a sister-group of the aspinine assemblage (*sensu* Howes, 1978) it became evident that a group of taxa including *Phoxinus* possessed a suite of synapomorphies. It was also evident that some taxa currently recognised as synonyms of *Phoxinus* are valid genera. A definition of *Phoxinus* is presented here with a critique of former synonymies, together with a revised synonymy. In addition notes are included on the possible relationships of *Phoxinus*, and, in the light of the revised synonymy, the geographical distribution of the genus.

List of study material

Abbreviations: AMNH, American Museum of Natural History; BMNH, British Museum (Natural History); CAS, Californian Academy of Sciences; FMNS, Field Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum.

The taxonomic and anatomical descriptions in this paper are based on the following specimens. In addition, material listed in Howes (1978) was used for out-group comparisons.

Acahara semotilus, syntypes, USNM 45227.
Couesius plumbeus, BMNH1893.2.7:637–645; 1935.4.21:2–5; UMMZ 133303; 145587.
Eupallasella percnurus. BMNH 1893.1.27:14–17; 1895.10.14:70–73; 1925.8.6:24; *E. percnurus stagnalis* 1899.7.25:36.
Hybognathus hankinsoni, BMNH 1973.2.3:48–57.
Lagowskiella lagowskii, BMNH 1974.8.6:21–30: 1923.8.6:23; USNM 76732; 76726; 76722; 82303; 48937; 105173; 105215.
Oreoleuciscus humilis, BMNH 1974.8.6:63–72.
'Phoxinellus' callensis, BMNH 1912.5.29:1–7.
'Phoxinellus' epiroticus, BMNH 1979.2.21:161.
'Phoxinellus' ghetaldii, BMNH 1903.12.4:37–40.
'Phoxinellus' pstrossi, BMNH 1911.9.28:4–5, syntypes.
'Phoxinellus' metohiensis, BMNH 1911.9.22:12–13, syntypes.
Phoxinus cumberlandensis, UMMZ 201152.

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Issued 28 February 1985

Phoxinus eos, UMMZ 185407.
Phoxinus erythrogaster, BMNH 1972.2.3:11–20; 21–32; 1982.4.13:4311–320; UMMZ 144867.
Phoxinus neogaeus, BMNH 1963.10.28:56–60: UMMZ 108044.
Phoxinus oreas, BMNH 1983.8.19:33–34.
Phoxinus phoxinus, BMNH 1974.8.6:31–42 (Mongolia); 1968.11.5:47–63; 1969.1.24:139–554; 1974.8.6:31–42; 43–62; 1982.11.15.22–33 (all U.K. localities).
'Phoxinus' czekanowskii, BMNH 1871.7.19:22–23.
'Phoxinus' poljakowi, BMNH 1849.7.25:34.
Pseudaspius bergi, CAS(SU)22393; FMNS 55801 (all syntypes).
Rhynchocypris costatus AMNH 10917; 10909; 10914.
Rhynchocypris steindachneri BMNH 1891.10.15; 1907.12.23:11–14; UMMZ 202118.
Rhynchocypris oxycephalus, BMNH 1895.5.31:41–43; 1910.6.30:63–64.
Rhynchocypris variegatus, BMNH 1889.6.8:97–106 (syntypes)
Semotilus atromaculatus BMNH 1982.4.13:4531–40.
Tribolodon jouyi USNM45228 (syntypes); BMNH 1907–12.10:57–62.

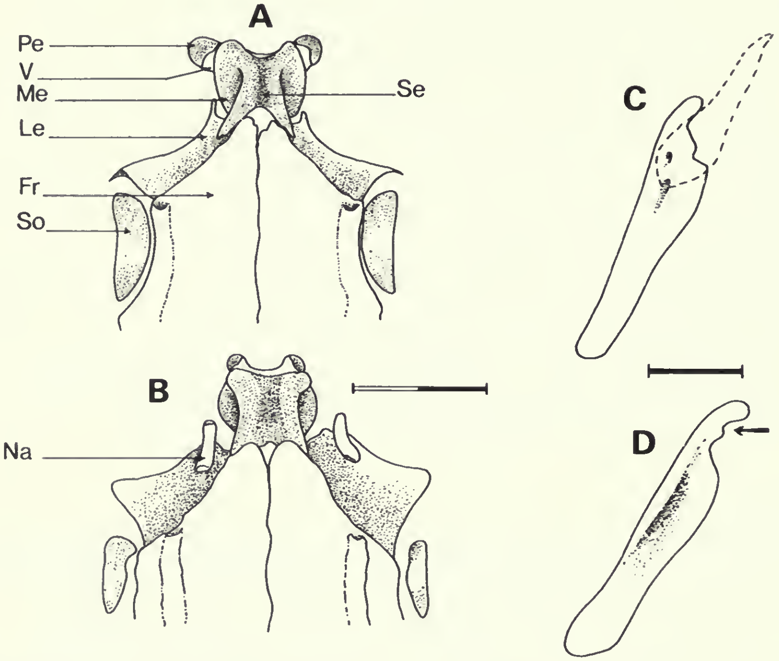

Fig. 1 Dorsal views of the ethmoid regions of A, *Phoxinus phoxinus*; B. *Ph. erythrogaster*. Supracleithrum of, C. *Ph. phoxinus* in lateral view (dashed line indicates posttemporal); D. *Ph. erythrogaster* in medial view. Arrow indicates dorsal notch. Fr = frontal; Le = lateral ethmoid; Me = mesethmoid; Na = nasal; Pe = preethmoid; Se = supraethmoid; So = supraorbital; V = vomer. Scales in mm.

Definition of *Phoxinus*

Comparative analysis with a wide range of cyprinid taxa has indicated that the following characters are synapomorphic for the included species: supraethmoid elongate, narrow-waisted; dorsal tip of supracleithrum formed into a notch, the upper part articulating with a medial shelf or process of the posttemporal (Fig. 1C;D); supraorbital minute; nasal reduced (in some individuals of *Phoxinus phoxinus* to an epidermal canal) and widely separated from the anterior frontal canal opening (Fig. 1B); diagonal rows of comb-like scales in the pectoral area which in breeding males are tuberculate (Fig. 2A–C); scales absent from the abdominal region in some species.

Diagnosis: Fishes of adult size up to 120 mm SL, body elongate, terete (depth, Mean of included species is 30% of standard length); mouth horizontal or slightly oblique; jaw bones shallow, maxilla slender, spear-shaped; dentary without symphysial process, coronomeckelian bone (sesamoid articular) well-developed elongate and spear-shaped, often with a broad medial flange; olfactory foramen small, almost entirely within the lateral ethmoid, with, in some species, the upper border of the foramen produced forward as a bony flange; palatine laterally flared; pterosphenoids separated from oneanother by the optic foramen; infraorbitals reduced; dermosphenotic present; subtemporal fossa small, ovate or ellipsoidal and often with an anterior extension into the pterotic, roofed mainly by the epioccipital (Fig. 3A); posttemporal fossa absent; supraoccipital crest absent; no connection between the preopercular and supraorbital sensory canals; intercalar well-developed, sometimes with a posterior process; coracoid strut-like; symphysis of the cleithrum club-shaped; scales usually small, 60 to more than 90 in the lateral-line; olfactory lamellae finger-like, 20–30; gill-rakers few, 5–10 (rarely 11 or 12) on 1st ceratobranchial; anterior part of 1st ceratobranchial covered by epithelial tissue sealing it closely to the hyoid bar, leaving only a small gap between the bucco-pharyngeal and opercular cavities; shallow neural complex on 3rd vertebrae; 2 or 3 feebly developed anterior supraneurals; mean number of vertebrae (for all species) 38; marked sexual dimorphism expressed in breeding coloration and the diagonal rows of modified, comb-like scales on the pectoral regions of ripe males and females (Fig. 2); lips often highly papillose and buccal roof tissue furrowed and tuberculate (Figs 7A–E).

In view of the above re-definition, the currently accepted concept of *Phoxinus* requires revision. This concept has been based principally on the works of Berg and Bănărescu.

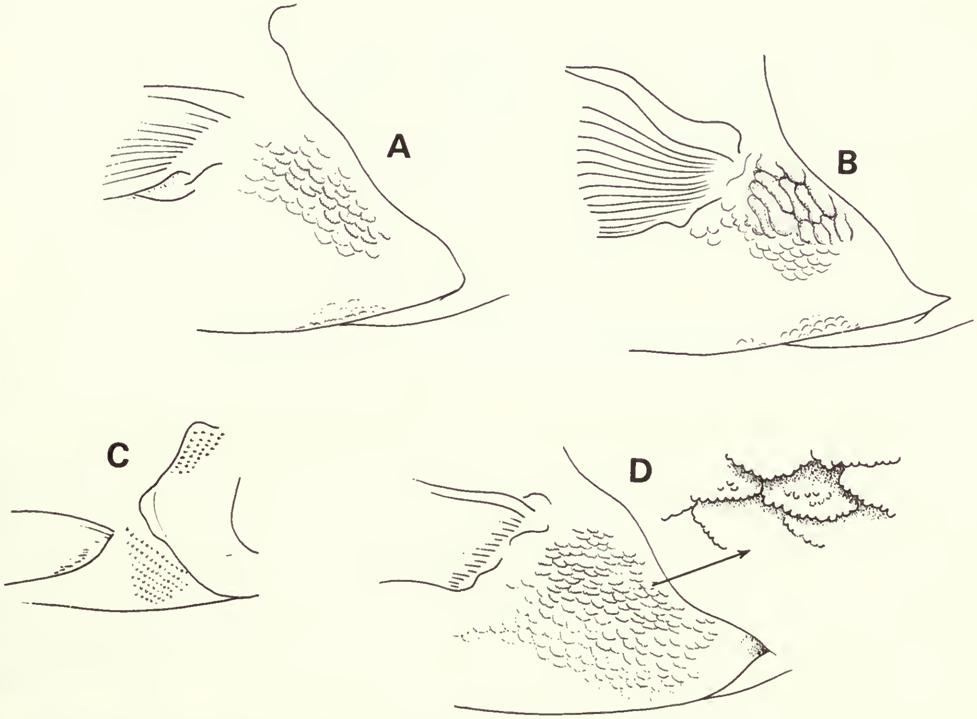

Fig. 2 Pectoral squamation in ripe males (comb-scales) of A, *Phoxinus phoxinus* BMNH 1968.11.5: 47–63, 55·5 mm SL; B. *Ph. neogaeus* BMNH 1963.10.28: 56–60, 68·5 mm SL; C. *Ph. erythrogaster* UMMZ 144867, 42·5 mm SL, also showing 'prickles' on operculum; D. *Couesius plumbeus* BMNH 1935.4.21: 2–5, 84 mm SL, with some scales magnified to 50 × .

Critique of generic synonymies of Berg and Bănărescu

Berg's synonymies

The synonymy given by Berg (1949) is with some additions, basically that published in 1912, and has been widely accepted. Its acceptance has, however, been uncritical and a close analysis of the included taxa leads to substantial modification.

Berg listed as synonyms of *Phoxinus* the following: *Gila* Baird & Girard, 1854; *Rhynchocypris* Günther, 1889; *Eulinneela* Dybowski, 1916; *Lagowskiella* Dybowski, 1916; *Eupsallasella* Dybowski, 1916; *Czekanowskiella* Dybowski, 1916; *Pfrille* Jordan, 1924 and *Moroco* Jordan & Hubbs, 1925.

Of his two included nearctic genera, *Gila* is recognised as a distinct taxon (see Miller, 1945) and *Pfrille* is generally regarded as a synonym of *Chrosomus* (see discussion and synonymy below, and Scott & Crossmann, 1973: 397).

Of the other included taxa, *Eulinneela* is here accepted as a synonym of *Phoxinus* (see p. 66) but *Rhynchocypris, Eupallasella, Lagowskiella, Czekanowskiella* and *Moroco* are not. Reasons for their exclusion from synonymy and their recognition as distinct taxa are as follows:

RHYNCHOCYPRIS Günther, 1889

TYPE SPECIES: *Rhynchocypris variegatus* Günther, 1889 (= *Pseudophoxinus oxycephalus* Sauvage & Dabry, 1874).

This is a distinctive taxon characterised by the following apomorphies: fleshy rostral process, most highly developed in ripe females (Fig. 4), hypertrophied olfactory lamellae with crenate ventral margins; attenuated posterior border of the operculum and a distinct notch in the dorsal border of the upright part of the cleithral lamellae.

Berg (1912) recognised, correctly, that *Rhynchocypris variegatus* Günther, 1889 was a synonym of *Pseudophoxinus oxycephalus* Sauvage & Dabry, 1874. However, he also recognised *oxycephalus* as a subspecies of *Phoxinus lagowskii* Dybowski, 1869. This is incorrect, since *Phoxinus lagowskii* represents a taxon quite distinct from *Rhynchocypris oxycephalus* (see p. 63).

Rhynchocypris oxycephalus has been disregarded by many authors and appears in the literature under the following erroneous combinations: *Leuciscus brandti* Fowler, 1899; 1924; *Phoxinus percnurus sachaliensis* Berg, 1906; *Phoxinus lagowskii variegatus* Berg, 1912; *Pseudaspius modestus* Jordan & Metz, 1913; *Ph. lagowskii chorensis* Rendahl, 1928; *Moroco variegatus* Mori, 1930; *Moroco variegatus septentrionalis* Mori, 1930; *Moroco oxycephalus* Mori, 1930; *Ph. lagowskii variegatus,* Berg, 1932; *Ph. lagowskii oxycephalus* Berg, 1932; 1949 (part; Takema River).

ie what was Ph. [illegible]

Two other species of *Rhynchocypris* are recognised here; *R. steindachneri* (Sauvage, 1883) and *R. costatus* (Fowler, 1899). Both species differ from *R. oxycephalus* in being shallower bodied and in having fewer gill-rakers on the 1st ceratobranchial and a different body colour-pattern (Fig. 5B).

2 *Rhynchocypris steindachneri* has a shorter head than that of *R. oxycephalus* and modally shorter than that of *R. costatus;* it also has a greater interorbital width than the two latter species; see Table I. The lateral line scale count in *R. steindachneri* is less than in *R. oxycephalus* (80–88) and *R. costatus* (80–84). Characteristic body markings of *R. steindachneri* comprise dark mottling overlying a deep lateral band; the head and snout are dark (Fig. 5A).

The following synonyms are those recognised by Okada (1960) under *Moroco steindachneri: Phoxinus steindachneri* Sauvage, 1883; *Hemitremia steindachneri,* Jordan, Tanaka & Snyder, 1913; *Leuciscus steindachneri,* Jordan & Snyder, 1901; *Leuciscus dorobae* Ishikawa, 1904; *Pseudaspius atrilatus* Jordan & Thompson, 1914; *Moroco steindachneri,* Jordan & Hubbs, 1925; Okada, 1960; *Moroco yamamotis* Jordan & Hubbs, 1925.

3 *Rhynchocypris costatus* is immediately distinguished from its congeners by its elongate body, longer operculum and high vertebral number (see Table 1). The body markings show less mottling than in *R. oxycephalus* and there is a deeper lateral band than in *R. steindachneri* (Fig. 5c).

Since it was originally described by Fowler (1899) as *Leuciscus costatus*, the species has been recognised as a synonym of *Phoxinus lagowskii oxcephalus* by Fowler (1924), Mori (1934), Berg (1912:1949) and by Nichols (1928). Mori (1934 : 24–27) described both *Phoxinus oxycephalus* and *Ph. lagowskii* from Jehol (N.E. China). However, his figures of these species (P1.X, figs 1 & 2) depict, respectively, female and male specimens of *R. costatus*. The *Ph. lagowskii oxycephalus* from Suifin reported by Dulckeit (1927) is also possibly *R. costatus*.

Although all the American Museum specimens are labelled as *Rhynchocypris costatus* (apparently by Nichols), this combination does not appear to have been published, and to my knowledge is done so here for the first time.

Table 1 Morphometric and meristic comparisons between *Rhynchocypris* species

	oxycephalus		*steindachneri*		*costatus*	
	Range (10 specimens, 81–105 mm SL)	M	Range (5 specimens, 76·5–87·3 mm SL)	M	Range (25 specimens, 51–135 mm SL)	M
% of SL:						
D	20·7–24·0	22·5	20·0–23·2	21·8	16·6–21·5	17·1
H	26·0–28·0	26·8	22·8–25·9	25·1	23·2–29·4	26·9
D–S	53·8–56·7	55·3	53·9–56·7	50·7	48·5–57·0	53·2
CpL	20·5–24·0	22·7	23·4–25·1	23·9	20·7–29·6	24·2
CpD as % of its length:						
	48·0–61·0	52·4	45·0–50·0	48·8	31·4–48·9	43·5
% of head length:						
IO	28·0–35·2	31·7	32·4–36·3	34·5	26·9–32·8	29·4
Sn	28·6–35·2	31·0	29·5–33·0	31·2	25·0–32·7	29·6
Ey	16·4–21·5	19·7	21·0–24·3	22·6	19·2–26·5	23·0
GR	1–2/5–7		2/4–5		2–3/4–5	
Ll	80–88		70–80		80–84	
Vertebrae	36 total (4+17–18+1)		37–38 (4+17–18+19+1)		42–44 (4+19–20+18–20+1)	

D = body depth; H = head length (not including rostral process); D–S = distance between snout and 1st dorsal fin ray; CpL, CpD = caudal peduncle length and depth; IO = interorbital width; Sn = snout length (not including rostral process); Ey = eye diameter; GR = gill-rakers on epibranchial/ceratobranchial; Ll = lateral line scales. Vertebral counts are the 4 Weberian vertebrae, abdominal, caudal and fused preural–ural centrum.

EUPALLASELLA Dybowski, 1916

TYPE SPECIES: *Cyprinus percnurus* Pallas, 1811.

Dybowski (1916) recognised the distinctiveness of *Phoxinus percnurus* by placing it in a separate genus, *Eupallasella* but Berg (1912; 1949) treats this taxon as a synonym of *Phoxinus*.

Gasowska (1979) made an osteological comparison of *Ph. percnurus* and *Ph. phoxinus*, concluding that *Ph. percnurus* was distinct enough to warrant its assignment to a separate genus. In her opinion, *Ph. percnurus* was closely related to *Rhynchocypris oxycephalus*. However, her uncritical acceptance of Berg's synonymy of *R. oxycephalus* with *Moroco bergi* (Jordan & Metz, 1913) caused her to refer *percnurus* to the genus *Moroco*. In fact, *Moroco* is a synonym of *Lagowskielia* see p. 63 below) and *Ph. percnurus* shares none of those characters which define that genus.

Of the osteological characters differentiating *Ph. percnurus* from *Ph. phoxinus* listed by Gasowska (1979), those for *percnurus* appear to be plesiomorphic (*i.e.* broad supraethmoid and supraorbital; pentagonal 1st infraorbital; shallow urohyal median plate; symmetrical neural complex; short operculum with rounded border). Of the other morphological characters which Gasowska lists, the mouth shape is significantly different. In *Ph. phoxinus* the mouth is subterminal, almost horizontal and with the lower jaw articulation beneath the anterior margin of the orbit. In *Ph. percnurus* the mouth is terminal, the lower jaw obliquely aligned with its articulation anterior to the orbital border, (Fig. 6).

Phoxinus percnurus lacks the characteristic pectoral 'comb scales' and naked abdomen of *Phoxinus (sensu stricto)* and also lacks those synapomorphies characterising the other genera considered here although the presence of an interpelvic flap, strongly imbricate scales and a mottled body pattern are characteristics shared with *Rhynchocypris*. *Phoxinus percnurus* has, however, a significantly greater body depth than any *Rhynchocypris* species or *Phoxinus* species, it being 25·9–29·4% of SL (*cf.* Table 1). There are also a higher number of gill-rakers in *percnurus* (8–9 on the 1st ceratobranchial) than in *Rhynchocypris* and the Eurasian *Phoxinus* species (*phoxinus; brachyurus*).

Since certain osteological and other morphological characters exclude *percnurus* from both *Phoxinus* and *Rhynchocypris* (see above) I refer the species to its former genus, *Eupallasella*. Berg (1949) lists six subspecies of *E. percnurus*. Of these, the Sakhalin minnow, *percnurus sachaliensis* is referred to *Rhynchocypris oxycephalus* (see p. 60).

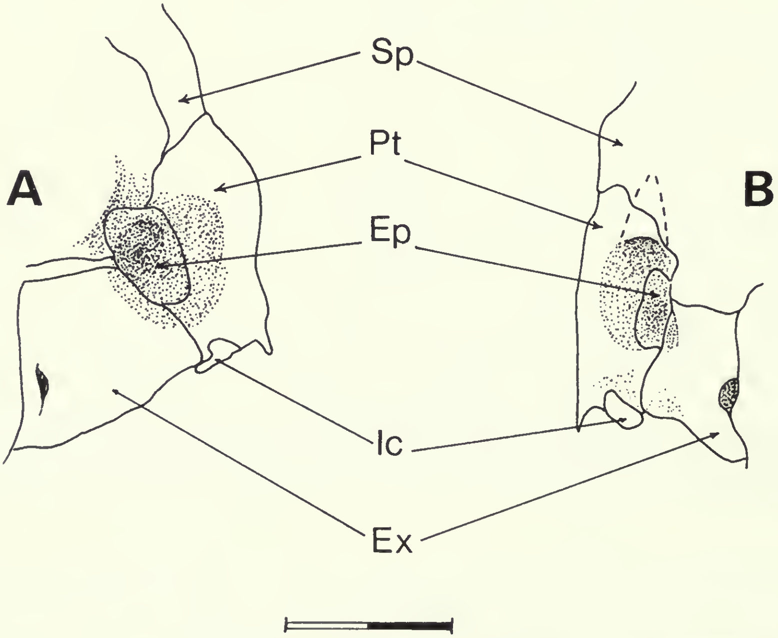

Fig. 3 Subtemporal fossae of A. *Phoxinus phoxinus* and B. *Lagowskiella lagowskii*. Dashed line indicates anterior chamber of fossa. Ep = epioccipital; Ex = exoccipital, Ic = intercalar; Pt = pterotic; Sp = sphenotic. Scale in mm.

MOROCO Jordan & Hubbs, 1925

TYPE SPECIES: *Pseudaspius bergi* Jordon & Metz, 1913 (= *Phoxinus lagowskii* Dybowski, 1869).

Having examined syntypes of *Pseudaspius bergi* (CAS(SU)22393, 92 mm SL and FMNS 55801, 59 & 61 mm SL, all from Chinnampo, Korea), I agree with Berg (1949) that this taxon is a synonym of *Phoxinus lagowskii* Dybowski, 1869. Although Jordan & Metz (1913) give a lateral line scale count of '... 100', I count 86 scales in the types, cf. 72–87 in *Ph. lagowskii.* Berg is wrong, however, in assigning the species *lagowskii* to *Phoxinus.* This species shares none of the derived characters that define *Phoxinus* species, and differs from those species in the following features:

Character	*'Phoxinus' lagowskii*	*Phoxinus (sensu stricto)*
Supraethmoid	broad with a V-shaped notch	narrow with a shallow notch
Nasal	elongate	short
Supraorbital	large	minute
Infraorbitals 4 & 5	slightly divergent from orbit	vertical
Dilatator fossa incorporates	sphenotic	pterotic and sphenotic
Orbitosphenoid	elongate, extensive contact with parasphenoid	short, minimal contact with parasphenoid
Operculum	elongate with attenuated lower posterior border	almost square with rounded border
Supracleithrum	elongate, without notch	short, with dorsal notch (Fig .1c)
Subtemporal fossa	epioccipital reduced, anterior extension into the sphenotic and pterotic (Fig. 3B)	epioccipital forms major part of roof; short anterior extension into the pterotic (Fig. 3A)
Posterior cleithral lamina	short	long
Gill-rakers	thin, with crenate and papillate medial border; 8–9 on ceratobranchial	short and fleshy
Total vertebrae	40–44	36–40

In addition, *lagowskii* has a broader and longer post-orbital cranial region, a more elongate body and posteriorly placed anal fin than any *Phoxinus* species (Fig. 5D). The apomorphic gill-raker morphology, cranial elongation, anterior extent of the subtemporal fossa, attenuated operculum and high vertebral number are features shared with aspinine cyprinids (see Howes, 1978; 1984). Only the lack of a pterosphenoid origin for the *adductor arcus palatini* muscle precludes its inclusion within the aspinine group, and thus it appears as the sister-lineage to that assemblage.

Since it lacks *Phoxinus* synapomorphies and possesses those characters which affiliate it with the aspinines, the species *lagowskii* is referred to the genus *Lagowskiella* Dybowski, 1916, originally established as a subgenus of *Phoxinus* to contain this species. *Moroco* is thus recognised as a junior synonym of *Lagowskiella*; of those species formerly referred to *Moroco, steindachneri* Sauvage, 1883 is considered to be a species of *Rhynchocypris* (see above) and *jouyi* Jordan & Snyder, 1901 is recognised as a species of *Tribolodon* due to its ethmoid morphology being synapomorphic with species of that genus. The synonymy of *Lagowskiella* is as follows:

LAGOWSKIELLA Dybowski, 1916

TYPE SPECIES: *Phoxinus lagowskii* Dybowski, 1869.

Moroco Jordan & Hubbs, 1925 (type *Pseudaspius bergi* Jordan & Metz, 1913)
?*Czekanowskiella* Dybowski, 1916 (subgenus of *Phoxinus*; type: *Ph. czekanowskii* Dybowski, 1869).

Lagowskiella lagowskii is distributed in the Amur, basin of the Lena, basins of Lake Khanka, Ussuri, Khor, Sungari and in Korea. The citations to *Phoxinus lagowskii* given in Berg (1949) and that listed in Berg (1909, Fishes of the Amur) are taken to refer to this species. The *Phoxinus lagowski* (sic) subspecies of Mori (1928) from the Yalu river, Korea is possibly also this species. *Phoxinus poljakowi, Ph. czekanowskii, Ph. dementjevi* and *Ph. grumi* should probably also be referred to *Lagowskiella* (see p. 67 below).

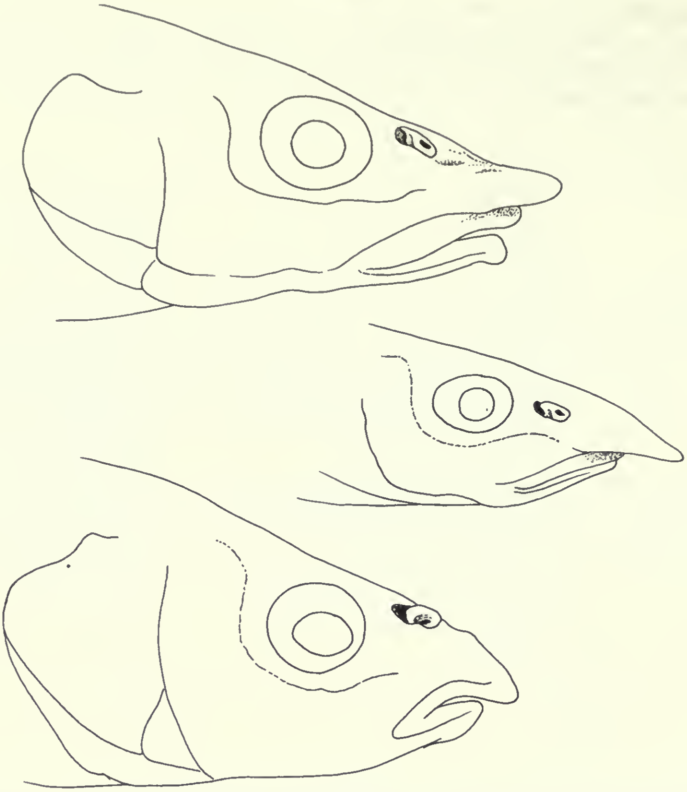

Fig. 4 Head profiles, showing rostral extension of, above, *Rhynchocypris oxycephalus* (syntype of *R. variegatus*) BMNH 1889.6.8: 97–100, 108 mm SL: centre, *R. steindachneri,* ripe female, UMMZ 202118, 83 mm SL: below, *'Phoxinellus' pstrossi,* female BMNH 1911.9.28: 4–5, 87 mm SL.

Bănărescu's synonymy

Bănărescu (1964) followed Berg's (1949) synonymy of *Phoxinus* although he omitted *Gila* (which he recognised as a subgenus of *Leuciscus*) and Dybowski's various taxa. Bănărescu recognised *Chrosomus* as a subgenus of *Phoxinus,* thus admitting, as a consequence, four nearctic species to *Phoxinus, viz: neogaeus, oreas, erythrogaster* and *eos.* Two others were added subsequently *Ph. margarita* (Cope, 1868) by Legendre (1970) and *Ph. cumberlandensis* by Starnes & Starnes (1978); see below, p. 68.

Bănărescu's synonymisation of *Chrosomus* and *Phoxinus* has evoked varying responses, with acceptance, or partial acceptance by some authors (Bailey *et al.,* 1970; McPhail & Lindsey, 1970; Legendre, 1970; Starnes & Starnes, 1978) and rejection by others (Scott & Crossmann, 1973, see quotation above, p. 57; Gasowska, 1979; Howes, 1981).

Detailed studies of the comparative osteology of *Phoxinus* and *Chrosomus* have been published respectively by Mahy (1975) and Gasowska (1979), Mahy's work demonstrated minimal differences between species of the two genera and supported Bănărescu's synonymy. Mahy maintained that *Chrosomus neogaeus* was more closely related to *Phoxinus phoxinus* than to other *Chrosomus* species. Gasowska rejected the synonymy of Bănărescu and claimed to show marked osteological differences between *Phoxinus* and *Chrosomus.* Taking a step even further, Gasowska introduced the genus *Parchrosomus* for the species *Chrosomus oreas.* Her recognition of genera, however, is dependent mainly upon differences in the shape of the basioccipital pharyngeal process. Such variability in the process is well within that of other cyprinid genera (pers. obs.) and cannot, on its own, be used as a 'generic' character. Gasowska does not assign any polarity to the osteological differences she recognises, and ultimately separated the genera largely on alimentary canal length and body coloration. Although Gasowska points out the apomorphic nature of the pectoral squamation in *Ph. phoxinus*, she does not recognise its presence in *'Chrosomus'* species.

Howes (1981) opined that *Phoxinus* and *Chrosomus* were distinct genera, on the basis of what was regarded as a synapomorphic neural complex in *Chrosomus* species. Further examination of the osteology of several *Phoxinus* species reveals that this character is variable within the framework of other synapomorphies (see p. 58). Thus, on derived osteological and other characters there is no reason to maintain the separation of *Phoxinus* and *Chrosomus*.

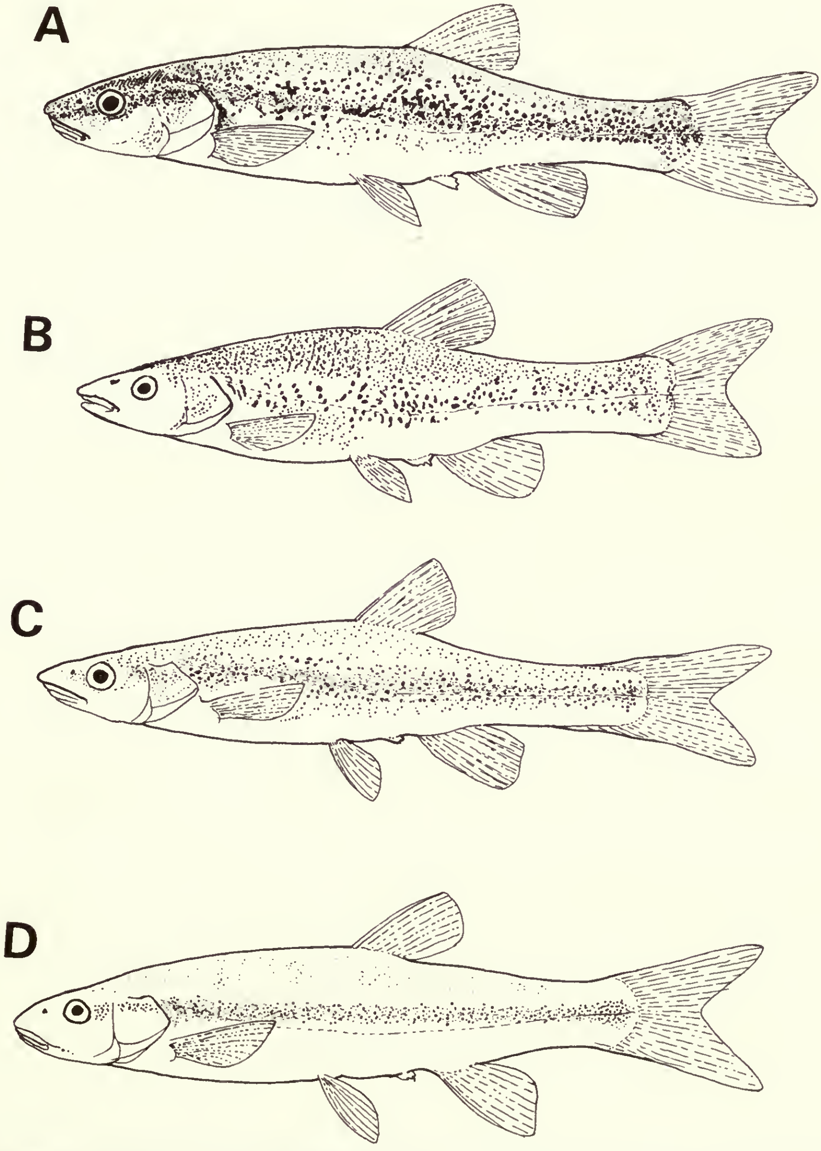

Fig. 5 Outline drawings showing pigment patterns in A, *Rhynchocypris steindachneri*; B, *R. oxycephalus*; C, *R. costatus*; D, *Lagowskiella lagowskii*.

A revised synonymy of *Phoxinus*

PHOXINUS Rafinesque, 1820

TYPE SPECIES: *Cyprinus phoxinus* Linnaeus, 1758, *Syst. Nat.* 10th ed.: 322 (Europe).

Chrosomus Rafinesque, 1820, *Ichthyologia Ohiensis*: 47 (type species: *C. erythrogaster* Raf., 1820)
Eulinneella Dybowski, 1916, *Pamietn. Fizjograf.* **23:** 101 (subgenus, type species: *Ph. phoxinus* Linn.)
Pfrille Jordan, 1924, *Copeia,* **1924:** 71 (type species: *Ph. neogaeus* Cope, 1869)
?*Acahara* (Jordan & Hubbs, 1925, *Mem. Carnegie Museum* **10** (2): 177 (type species: *Richardsonius semotilus* Jordan & Starks, 1905)
Parchrosomus Gasowska, 1979. *Annales zoologici Warszawa* **34** (12): 404 (type species: *Chrosomus oreas* Cope, 1868)

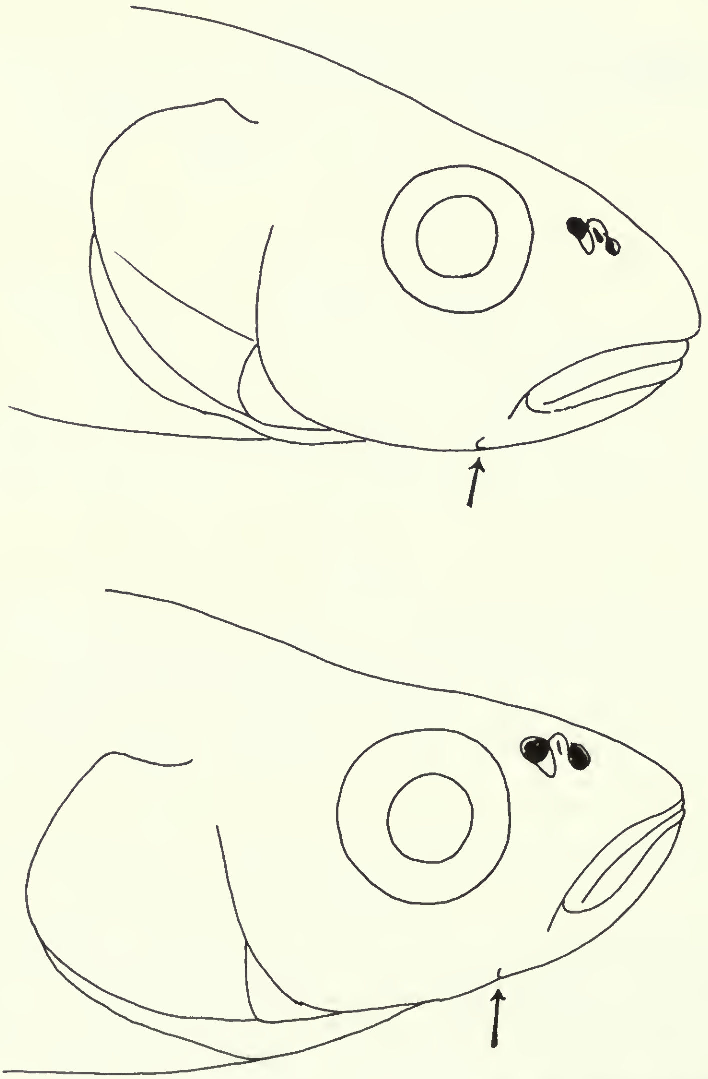

Fig. 6 Head profiles showing mouth–jaw position in, above, *Phoxinus phoxinus* BMNH 1969.1.24: 139–554, 55·5 mm SL; below, *Eupallasella percnurus* BMNH 1925.8.6: 24, 75 mm SL. Arrows indicate lower jaw articulation.

Notes on this synonymy

The reasons for including *Chrosomus* with *Phoxinus* have been discussed above (p. 64); *Pfrille* is a junior synonym of *Chrosomus* and thus of *Phoxinus*.

Acahara was first used as a generic name by Mori (1930) and derived from the manuscript label of Jordan & Hubbs. Mori did not offer a diagnosis of the genus but referred to it the species *Richardsonius semotilus* Jordan & Starks ,1905, and *Telestes brandti* Dybowski, 1872. When Jordan & Hubbs (1925) defined *Acahara* they chose *Richardsonius semotilus* as the type species to conform with Mori's previous orthotypy. Their description of the genus appears, however, to be based not on the species *semotilus* but on *Telestes brandti*, now generally regarded as belonging to the genus *Tribolodon*.

Ikeda (1938) first considered *Acahara semotilus* to be a synonym of *Tribolodon brandti*, believing that Jordan & Stark's specimens were juveniles of that species. Ikeda's synonymy was followed by Berg (1949) and Okada (1960), although Lindberg & Legeza (1965) regard *Acahara* as a synonym of *Leuciscus*. These synonymies are, however, erroneous because *Acahara semotilus* possesses features which are quite distinct from those of any *Tribolodon* or *Leuciscus* species. In the syntypes of *Acahara semotilus* (USNM 45227, 66–190 mm SL), the bucco-pharyngeal and opercular cavities communicate through only a small opening, and there are only 2–3 gill-rakers on the 1st ceratobranchial (cf. extensive bucco-branchial gap, and 13–21 gill-rakers in *Tribolodon*). The rakers also lack the crenate and papillate margin characteristic of *Tribolodon* (Howes, 1984). No osteological material is available for *Acahara* so it cannot be determined whether phoxinine skeletal synapomorphies are present. Neither is it known if comb-like breast scales are present in ripe males. In the morphology of the branchial arches and in their overall appearance, *Acahara semotilus* resembles species of *Phoxinus* more closely than those of any other genus. Until more material is available for detailed investigation, *Acahara* is questionably referred to the synonymy of *Phoxinus*.

Robins *et al.* (1980: 75) treated Gasowska's *Parchrosomus* as a synonym of *Phoxinus*, but without giving justification for this decision. Argument supporting Robins *et al.* rejection of this taxon is given above (p. 64).

Species recognised as belonging to *Phoxinus*

The following species are considered as belonging to the genus *Phoxinus*:

EURASIAN SPECIES: *Ph. brachyurus* Berg, 1912 (Ili basin); *Ph. phoxinus* (Linn., 1758), Europe (including the British Isles and Russia; see Berg, 1949 for distribution. *Ph. issykulensis* Berg, 1912. Lake Issyk-kul and drainage; *Ph. sedelnikowi* Berg, 1908. Basins of the Ili, Balkash and Issyk-kul.

Apart from *Phoxinus phoxinus* no specimens of the other three recognised Asian species have been available for examination and their inclusion is based solely on the characters given by Berg (1912; 1949), namely, the length of the jaw (in all species) and the naked abdomen (in *Ph. sedelnikowi*).

The central Asian species referred to *Phoxinus* by Berg (1912; 1932; 1949) *viz: poljakowi* and *czekanowskii*, should most probably be referred to the genus *Lagowskiella* (see above, p. 63). As *Ph. czekanowskii* is the type species of Dybowski's (1916) subgenus *Czekanowskiella*, that taxon is placed tentatively in the synonymy of *Lagowskiella* (p. 63).

Only a single specimen of *Ph. poljakowi* is available to me. It possesses a shallow lower jaw, attenuated operculum, somewhat divergent posterior infraorbitals, a large bucco-branchial aperture, and papillate gill-rakers. Similarly, *Ph. czekanowskii* has an attenuated opercular border and divergent infraorbitals, but the bucco-branchial opening is more restricted, as in *Phoxinus (sensu stricto)*; the specimens to hand are too poorly preserved to ascertain the morphology of the gill-raker membrane. No examples of the various *Ph. czekanowskii* subspecies recognised by Berg (1949) have been examined. The close resemblances between *Ph. poljakowi*, *Ph. czekanowskii* and *Lagowskiella lagowskii*, with the published descriptions of *Ph. dementjevi* Turdakov & Piskarev (1954) from the Chu River, Kazakhstan, and *Ph. grumi* Herzenstein (1889; in Berg, 1906) from Turfan Oasis, suggest that they all belong to *Lagowskiella*.

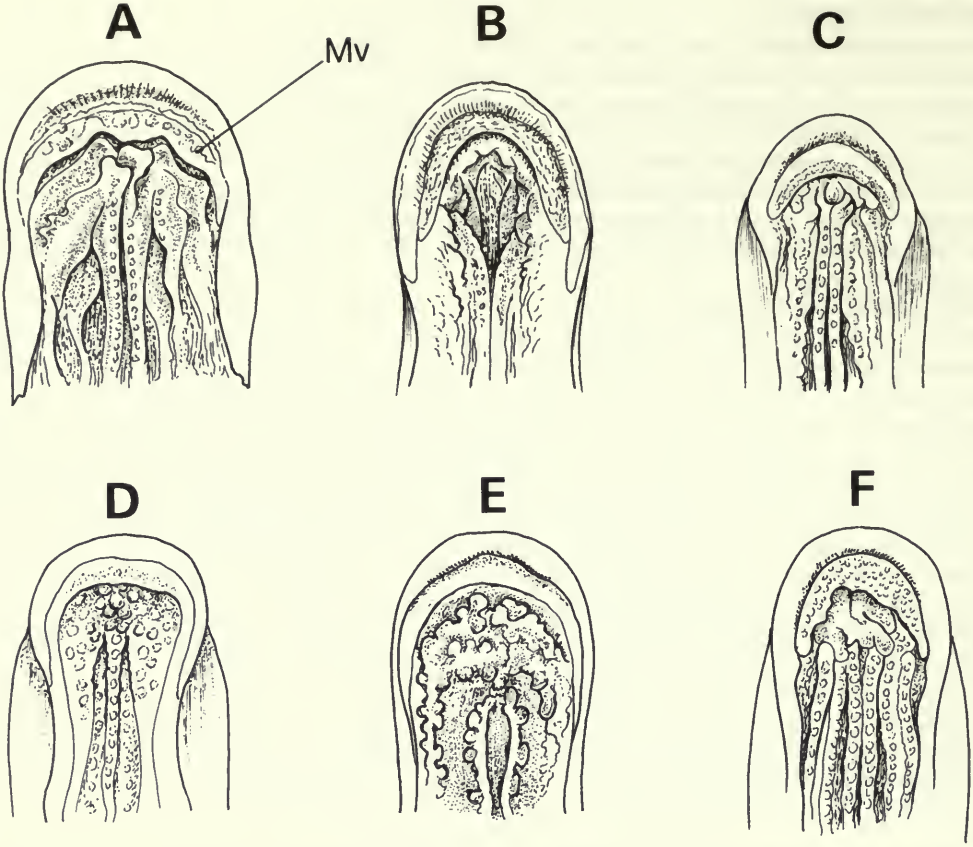

Fig. 7 Buccal roof tissue in A, *Phoxinus phoxinus*, BMNH 1974. 8.6: 43–62, 70 mm SL; B, *Ph. neogaeus*, UMMZ 108044, 54 mm SL; C, *Ph. eos* UMMZ 185407, 51·5 mm SL (n.b. Maxillary valve is papillate over half its width); D, *Ph. erythrogaster*, UMMZ 144867, 40·5 mm SL; E. *Ph. cumberlandensis*, UMMZ 201152, 50 mm SL (n.b. *Ph. oreas* has a similar morphology); F, *Couesius plumbeus*, UMMZ 133303, 74·5 mm SL. Mv = maxillary valve.

Nearctic species: Mahy (1975) recognised *Ph. neogaeus*, *Ph. eos* and *Ph. oreas* as races of a single species, *Ph. erythrogaster*, although this is not generally accepted by North American workers; see for example, Lee *et al.* (1980). Legendre (1970) considered, on the basis of chromosome numbers, that *Clinostoma margarite* Cope, 1868 belonged to *Phoxinus*. Lee *et al.* (1980) refer *margarita* to the genus *Semotilus*, an action with which I concur. Joswiak *et al.* (1980) reviewed the karyotypes of *Phoxinus* species and suggested that populational differences were exhibited in chromosome number. However, the authors admit that pairing of homologous chromosomes is partially subjective and that a chromosome may be misclassified owing to differential arm contraction. Their conclusion is that chromosome analysis '... does not clarify affinities within the genus'. The relationships between nearctic species are discussed below (p. 70).

Relationships and geographic distribution of *Phoxinus*

Relationships: The principal synapomorphy characterising *Phoxinus* species—the comb-like pectoral scales—occurs elsewhere only in the nearctic genus *Couesius*. As in *Ph. phoxinus*, the scales of *Couesius* have scalloped edges, and in ripe males cover an extensive area of the prepectoral region extending mesad to the midline (Fig. 2D). *Couesius* shares with *Phoxinus* species a derived form of buccal roof tissue, one that is deeply furrowed and papillate, and a heavily papillose maxillary valve; see below and Fig. 7F.

The comb-like breast scales in Eurasian *Phoxinus* have, for the most part, been overlooked. The otherwise comprehensive accounts of sexual dimorphism in *Phoxinus* by Frost (1943), Oliva (1953) and Lohinsky (1964) fail to note this character, but Gasowska (1979) used the feature to separate *Ph. phoxinus* from *Ph. percnurus* (referred here to *Eupallasella*; see p. 61). The presence of comb-like or tuberculate scales is well known amongst the nearctic *Phoxinus* species (see for example, Scott & Crossmann, 1973; Starnes & Starnes, 1978). In non-breeding male and female *Phoxinus,* belly scales are lacking and although there may be pre-pelvic scale patches they never meet in the midline. In the pre-pectoral area of non-breeding fishes, there are small tubercles (unculi of Roberts, 1982). There is a wide variation in the morphology of the breast 'scales' in *Phoxinus* species. Those in *Ph. erythrogaster* are smaller, having more the appearance of 'prickles' and are arranged in more regular rows than those of *Ph. phoxinus* (Fig. 2C), whereas those in *Ph. neogaeus* are cushion-like (Fig. 2B). In breeding males of all *Phoxinus* species a patch of tubercles is developed on the dorso-posterior corner of the operculum (Fig. 2C). In *Ph. phoxinus* there is an associated swelling of the opercular epithelium which forms a marked protuberance (see Lohinsky, 1964, fig. 2).

The development of the buccal roof tissue in *Phoxinus* and *Couesius* appears to be a derived feature. Although many cyprinid taxa have convoluted and furrowed mouth lining (e.g. *Barilius*) they lack the large 'tubercular' papillae (Fig. 7).

Osteologically, *Couesius* is very similar to *Phoxinus*; both taxa share a narrow ethmoid bloc, slender jaw bones and a spear-like coronomeckelian bone. *Couesius* differs from *Phoxinus* in its attenuate operculum, posteriorly extended cleithral lamina, belly completely covered with scales, and the presence of a posterior barbel. The barbel is unlike that of barbines, barbelled carps or of *Tinca,* and is a papillate appendage of the upper rictal tissue.

Although *Phoxinus* and *Couesius* may be regarded as sister groups, it is not possible to say, on the basis of known synapomorphies which is the more derived taxon. The relationships of the *Phoxinus–Couesius* lineage are also problematical. No synapomorphies have been identified that would denote sister-group relationship between this lineage and any of those taxa treated in this review. *Eupallasella* and *Rhynchocypris* have phoxinine-like features, particularly in having a small buccal-branchial aperture, small scales and pleated genital papilla; although it must be said that these features are mosaically distributed amongst cyprinid taxa and may, therefore be plesiomorphic. However, both genera share a mottled colour-pattern (Figs 5A–C) which is unusual in cyprinids, and may indicate their close relationship with one another. On the other hand, *Rhynchocypris* shares with *Lagowskiella* a derived form of male genital papilla whereby a conical projection carrying the spermatic duct to a terminal pore, extends beyond the anal orifice (Figs 8B; D). Females of both genera also possess a blind-ending conical fleshy projection (Fig. 8C). Two other taxa possess similar genital morphology; *Oreoleuciscus* and some species of Croatian *'Phoxinellus'* (Figs 8E; F). In these taxa, however, it is only the males of *Oreoleuciscus* and the females of*'Phoxinellus'* that share the derived conditions of their counterparts in *Rhynchocypris* and *Lagowskiella*. *Oreoleuciscus* females and *'Phoxinellus'* males lack the genital processes. On the basis of derived osteological and other characters it seems likely that *Lagowskiella* is related to the aspinine assemblage (see p. 63). *Rhynchocypris,* on the other hand, may have a closer affinity to the Croatian *'Phoxinellus'* and the phoxinines (*Phoxinus*+*Couesius*).

A more precise theory of relationships is hampered by inadequate knowledge of *Phoxinellus* species. Trewavas (1971) referred to both the alpha and the beta level taxonomic problems associated with *Phoxinellus*. The situation was not improved, and indeed was marred, by Karaman's (1972) revision of the genus. Karaman included in *Phoxinellus* several species which had originally been assigned to various rutiline and leuciscine genera; it is clear, however, that he is in error, as the following discussion indicates. Some Croatian species of *Phoxinellus* (*sensu* Karaman), referred to above and formerly assigned to *Paraphoxinus (pstrossi, ghetaldii, croaticus* and *metohiensis)* are not members of that genus and represent a distinct taxon (or taxa). *Phoxinellus (sensu stricto)* includes those species distributed throughout the Levant (*adspersus, zeregi*) and possibly the north African species *chaignoni, callensis* and *guichenoti,* which have no

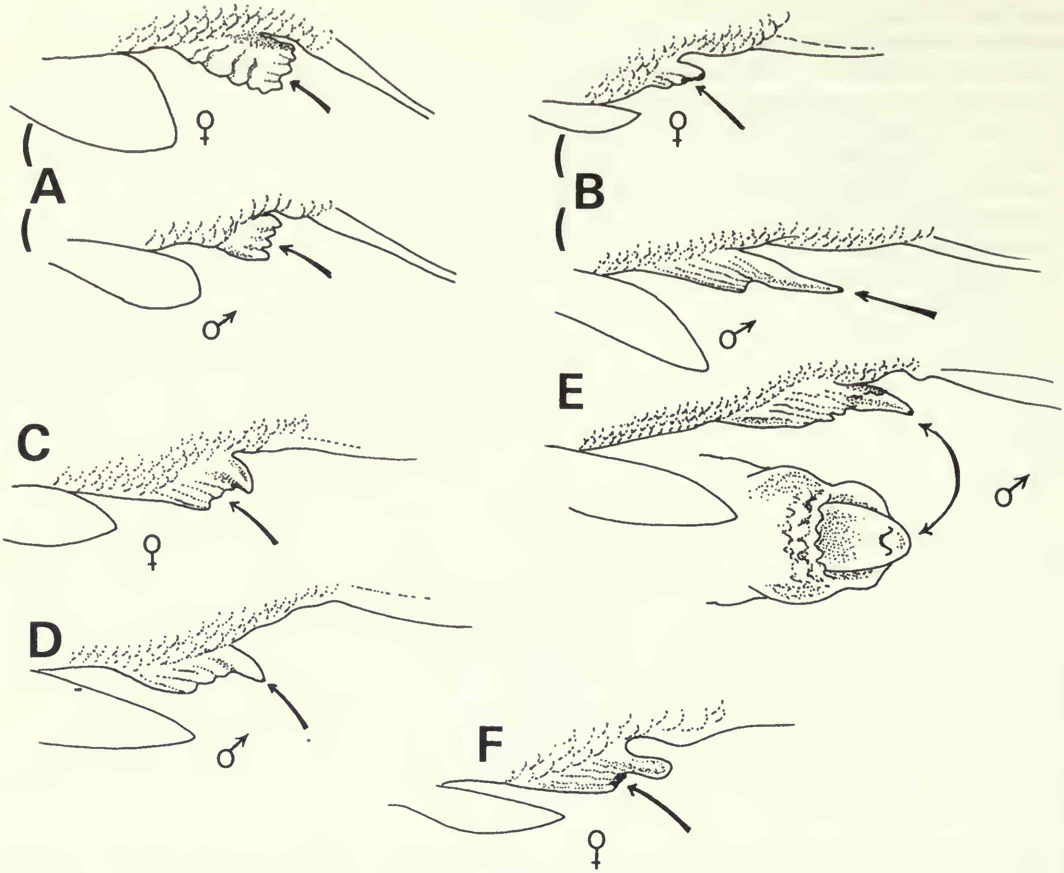

Fig. 8 Genital papillae shown in lateral views of A, *Phoxinus phoxinus*, ripe female, 72·5 mm SL and ripe male, 60 mm SL; B, *Lagowskiella lagowskii*, female, 70 mm SL and male, 70 mm SL; C, *Rhynchocypris oxycephalus*, ripe female, 92·5 mm SL; D, *Rhynchocypris steindachneri*, male, 47 mm SL; E, *Oreoleuciscus humilis*, male, 76·5 mm SL, also shown in ventral view; F, *'Phoxinellus' pstrossi*, ripe female, 87 mm SL. Arrows indicate position of genital orifice.

close relationship with either the Croatian *'Phoxinellus'* or with *Phoxinus*, but belong to a rutiline assemblage. The Croatian *'Phoxinellus'* share with *Phoxinus* absence of scales midventrally, and with *Rhynchocypris* an attenuated operculum, genital morphology, mottled colour pattern and, in some species, a fleshy rostal process (see Fig. 4). The relationships of the phoxinine lineage, *Phoxinus*+*Couesius* can only be established when a more complete study of the anatomy and taxonomy of the Croatian '*Phoxinellus*', *Rhynchocypris* and *Eupallasella* species have been undertaken.

Geographic distribution: Despite what may appear to be radical changes in the synonymy of *Phoxinus*, the distribution pattern is little different from that mapped by Bănărescu (1964, fig. 142). The only change is that the range given by Bănărescu for *Phoxinus phoxinus* now represents the range of the genus in Eurasia.

Regarding the nearctic species, both Legendre (1970) and Mahy (1975) account for the present distributional pattern by various post-glacial migrations and hybridisations. Mahy (1975) recognises *Ph. erythrogaster* as the plesiomorphic species (Mahy's 'primordial race'), and as having dispersed from its Mississippian refuge, whilst *Ph. neogaeus* dispersed over a more northerly area from its Missourian refuge. This of course presupposes that two taxa were specifically distinct prior to glaciation. If, on the other hand, *Ph. neogaeus* is considered to be the plesiomorphic North American species (as suggested by its broader ethmoid bloc and larger circumorbital bones), then its formerly widespread distribution can be seen, through the intervention of glacial episodes, to result in a disjunct pattern, the fragmented elements being represented by the derived extant species (or races, as recognised by Mahy).

Patterson (1981: 266) notes that theories of postglacial dispersal have been dominant in considering the distribution of North American fishes. It may be that the effects of glaciation were not so profound as to have extinguished the majority of species. Fewer propositions are necessary to argue that *Phoxinus* was widely dispersed across Asia and North America prior to glaciation than to suppose its subsequent dispersal. Mahy (1975) contended that *Ph. phoxinus* was more closely related to *Ph. neogaeus* than to the other North American species. This hypothesis has yet to be tested by cladistic analysis, the results of which will also provide a framework for testing vicariance as opposed to dispersal hypotheses of the species' distribution.

List of taxonomic changes

The following binominal combinations are those used by previous workers and those recognised in this study:

Species and author	Former generic assignment	Combination recognised in this paper
atrilatus Jordan & Thompson, 1914	*Pseudaspius*	*Rhynchocypris steindachneri*
bergi Jordan & Metz, 1913	*Pseudaspius*	*Lagowskiella lagowskii*
brachyurus Berg, 1912	*Phoxinus*	No change
brandti Dybowski, 1872	*Telestes*	*Tribolodon brandti*
brandti (*non* Dybowski) Fowler, 1899; 1924	*Leuciscus*	*Rhynchocypris oxycephalus*
chorensis (subspecies of *lagowskii*) Rendahl, 1928	*Phoxinus*	*Rhynchocypris oxycephalus*
costatus Fowler, 1899	*Leuciscus*	*Rhynchocypris costatus*
cumberlandensis Starnes & Starnes, 1978	*Phoxinus*	No change
czekanowskii Dybowski, 1869	*Phoxinus*	*?Lagowskiella czekanowskii*
dementjevi Turdakov & Piskarev, 1954	*Phoxinus*	*?Lagowskiella dementjevi*
dorobae Ishikawa, 1904	*Leuciscus*	*Rhynchocypris steindachneri*
eos Cope, 1862	*Chrosomus*	*Phoxinus eos*
erythrogaster Rafinesque, 1820	*Chrosomus*	*Phoxinus erythrogaster*
grumi Herzenstein, 1889	*Phoxinus*	*?Lagowskiella grumi*
issykkulensis Berg, 1912	*Phoxinus*	No change
jouyi Jordan & Snyder, 1900	*Leuciscus*	*Tribolodon jouyi*
jouyi, Okada, 1960	*Moroco*	*Tribolodon jouyi*
lagowskii Dybowski, 1869	*Phoxinus*	*Lagowskiella lagowskii*
lagowskii, Fowler, 1924	*Phoxinus*	*Rhynchocypris costatus*
lagowskii, Mori, 1934	*Phoxinus*	*Rhynchocypris costatus*
modestus Jordan & Metz, 1913	*Pseudaspius*	*Rhynchocypris oxycephalus*
neogaeus Cope, 1868	*Phoxinus*	No change
oreas Cope ,1868	*Chrosomus*	*Phoxinus oreas*
oxycephalus Sauvage & Dabry, 1874	*Pseudophoxinus*	*Rhynchocypris oxycephalus*
oxycephalus (subspecies of *lagowskii*) Berg, 1912; 1949	*Phoxinus*	*Rhynchocypris oxycephalus*
oxycephalus (subspecies of *lagowskii*) Dulckeit, 1927	*Phoxinus*	*?Rhynchocypris costatus*
oxycephalus, Mori, 1930	*Phoxinus*	*Rhynchocypris oxycephalus*
oxycephalus, Mori, 1934	*Phoxinus*	*Rhynchocypris costatus*
percnurus Pallas, 1811	*Phoxinus*	*Eupallasella percnurus*
percnurus, Gasowska, 1979	*Parchrosomus*	*Eupallasella percnurus*
phoxinus Linnaeus, 1758	*Phoxinus*	*Phoxinus phoxinus*
poljakowi Kessler, 1879	*Phoxinus*	*?Lagowskiella poljakowi*

sachalinensis (subspecies of *percnurus*) Berg, 1906	*Phoxinus*	*Rhynchocypris oxycephalus*
sedelnikowi Berg, 1908	*Phoxinus*	No change
semotilus Jordan & Starks, 1905	*Richardsonius*	*?Phoxinus semotilus*
semotilus, Jordan & Hubbs, 1925	*Acahara*	*?Phoxinus semotilus*
septentrionalis (subspecies of *variegatus*) Mori, 1930	*Moroco*	*Rhynchocypris oxycephalus*
steindachneri Sauvage, 1883	*Phoxinus*	*Rhynchocypris steindachneri*
steindachneri, Jordan & Snyder, 1901	*Leuciscus*	*Rhynchocypris steindachneri*
steindachneri, Jordan, Tanaka & Snyder, 1913	*Hemitremia*	*Rhynchocypris steindachneri*
steindachneri, Jordan & Hubbs, 1925	*Moroco*	*Rhynchocypris steindachneri*
steindachneri, Okada, 1960	*Moroco*	*Rhynchocypris steindachneri*
variegata Günther, 1889	*Rhynchocypris*	*Rhynchocypris oxycephalus*
variegatus, Mori, 1930	*Moroco*	*Rhynchocypris oxycephalus*
variegatus (subspecies of *lagowskii*) Berg, 1932	*Phoxinus*	*Rhynchocypris oxycephalus*
yamamotis Jordan & Hubbs, 1925	*Moroco*	*Rhynchocypris steindachneri*

Acknowledgements

I am greatly indebted to my colleagues, Humphry Greenwood, Keith Banister and Alwyne Wheeler for their critical reading of the various drafts of this paper. Also, to Margaret Clarke, James Chambers and Adrian Penrose for their various forms of assistance.

My sincere thanks go to Dr Reeve Bailey (UMMZ), Dr Gareth Nelson and Ms Norma Feinberg (AMNH), and Dr Richard Vari (USNM) for their warm hospitality and assistance during my visits to their respective institutions. Drs William Eschmeyer (CAS) and Don Stewart (FMNS) so kindly lent material in their care.

Many thanks are owed to the several colleagues too numerous to list, for the rewarding discussions on phoxinine taxonomy, particularly those friends at the ASIH meetings at De Kalb, Illinois in 1982.

References

Bailey, R. M., Fitch, J. E., Herald, E. S., Lachner, E. A., Lindsey, C. C., Robins, C. R. & Scott, W. B. 1970. A list of common and scientific names of fishes from the United States and Canada. *American Fisheries Society Special Publication* no. 6: 150 pp.

Bănărescu, P. 1964. *Fauna republicii populare Romine* **13:** 959 pp. Bucarest.

Berg, L. S. 1906 (1907). Notes sur quelques espèces palérctiques du genre *Phoxinus*. *Ezhegodnik zool. Muz. St. Petersburg.* **11:** 196–213.

—— 1912. Fauna Rossii, Ryby (Fauna of Russia, Fishes) **3:** 1–336. St. Petersburg.

—— 1932. *Freshwater fishes of the U.S.S.R. and adjacent countries.* (3rd edition) **1:** 543 pp.

—— 1949. *Freshwater fishes of the U.S.S.R. and adjacent countries.* (English translation of the 4th edition, 1964) **2:** 496 pp.

Coad, B. W. 1981. *Pseudophoxinus persidis*, a new cyprinid fish from Fars, southern Iran. *Canad. J. Zool.* **59** (11): 2058–2063.

Dulckeit, G. 1927. Contributions à la faune des poissons d'eau douce de la Sikhoté Aline. *Trudy Zool. Inst. Akad. Nauk. S.S.R.* Leningrad, **28**(2): 9–24.

Dybowski, B. 1869. Vorläufige Mittheilung über die Fischfauna des Ononflusses und des Ingoda in Transbaikalien. *Verh. zoool-bot. Gesel.* Wien **19:** 952.

—— 1916. Title unknown. *Pamietnik Fizyjograficzny.* Warsaw **23:** 100–102.

Fowler, H. W. 1899 (1900). Notes on a small collection of Chinese fishes. *Proc. Acad. Nat. Sci. Philad.* 179–182.

—— 1924. Some fishes collected by the third Asiatic expedition in China. *Bull. Amer. Mus. nat. Hist.* **50:** 388.

Frost, W. E. 1943. The natural history of the minnow *Phoxinus phoxinus*. *J. Anim. Ecol.* **12:** 139–162.

Gasowska, M. 1979. Osteological revision of the genus *Phoxinus* Raf., sensu Bănărescu 1964, with description of a new genus, *Parchrosomus* gen.n. (Pisces, Cyprinidae). *Annales Zoologici Polska Academia Nauk,* Warszawa (12) **34:** 371–409.

Günther, A. 1889. Third contribution to our knowledge of reptiles and fishes from the upper Yangtze-Kiang. *Ann. Mag. nat. Hist.* **4** (6): 218–229.

Herzenstein, S. M. 1889. *In:* G. Grum-Brzhimaĭlo. *Description of a journey to Western China.* **2:** 414. St. Petersburg.

Howes, G. J. 1978. The anatomy and relationships of the cyprinid fish *Luciobrama macrocephalus* (Lacepède). *Bull. Br. Mus. nat. Hist.* (Zool.) **34** (1): 1–64.

—— 1981. Anatomy and phylogeny of the Chinese Major carps *Ctenopharyngodon* Steind., 1866 and *Hypophthalmichthys* Blkr., 1860. *Bull. Br. Mus. nat. Hist.* (Zool.) **41** (1): 1–52.

—— 1984. Phyletics and biogeography of the aspinine cyprinid fishes. *Bull. Br. Mus. nat. Hist.* (Zool.) **47** (5): 283–303.

Ikeda, H. 1938. Statistical observations on the species *Tribolodon* in Japan and some notes on their distribution. *Science Reports of the Tokyo Bunrika Daigaku* **3** (Sect. B) No. 56: 163–192.

Ishikawa, C. 1904. Notes on some new or little known fishes of Japan. *Proc. Nat. Hist. Tokyo Museum* **1:** 1–17.

Jordan, D. S. & Hubbs, C. L. 1925. Record of fishes obtained by D. S. Jordan in Japan, 1922. *Mem. Carnegie Mus.* **10** (2): 93–346.

—— **& Metz, C. W.** 1913. A catalog of the fishes from the waters of Korea. *Mem. Carnegie Mus.* **6** (1): 1–65.

—— **& Snyder, J. O.** 1900. A list of fishes collected in Japan by Keinosuke Otaki and by the U.S. Steamer Albatross, with descriptions of fourteen new species. *Proc. U.S. natn Mus.* **23** (1235): 741–742.

—— **& Starks, E. C.** 1905. On a collection of fishes made in Korea by Pierre Louis Jouy, with descriptions of new species. *Proc. U.S. natn Mus,* **28** (1391): 193–212.

——**, Tanaka, S. & Snyder, J. O.** 1913. A catalogue of the fishes of Japan. *J. Coll. Sci. Imp. Univ. Tokyo* **33** (1): 1–431.

—— **& Thompson, W. F.** 1914. Record of the fishes obtained in Japan in 1911. *Mem. Carnegie Mus* **.6** (4): 205–313.

Joswiak, G. R., Starnes, W. C. & Moore, W. S. 1980. Karyotypes of three species of the genus *Phoxinus* (Pisces; Cyprinidae). *Copeia* **1980** (4): 913–916.

Karaman, M. S. 1972. Süsswasserfische der Türkei 9. Revision einiger kleinwüchsiger Cyprinidengattungen *Phoxinellus, Leucaspius, Acanthobrama* usw.aus Südeuropa, Kleinasien, Vorder-Asien und Nordafrika. *Mitt. Hamburg Zool. Mus. Inst.* **69:** 115–155.

Lee, D. S., Gilbert, C. R., Hocutt, C. H., Jenkins, R. E., McAllister, D. E. & Stauffer, J. R. 1980. *Atlas of North American freshwater fishes.* Public. N. Carolina Biol. Survey. 854 pp.

Legendre, P. 1970. The bearing of *Phoxinus* (Cyprinidae) hybridity on the classification of its North American species. *Can. J. Zool.* **48** (6): 1167–1177.

Lohinský, K. 1964. Prispevek k systematice a sexuálnimu dimorfismu strěvle ptoćni Phoxinus phoxinus (Linnaeus 1758). *Acta Musei Reginaehradecensis* Ser. A **6:** 221–246.

McPhail, J. D. & Lindsey, C. C. 1970. Freshwater Fishes of northwestern Canada and Alaska. *Bull. Fish. Res. Board Canada* **173:** 1–381.

Mahy, G. 1975. Ostéologie comparée et phylogénie des poissons cyprinoïdes III. Ostéologie comparée de *C. erythrogaster* Rafinesque, *C. eos* Cope, *C. neogaeus* (Cope) et *P. phoxinus* (Linné) et phylogénie du genre *Chrosomus. Naturaliste Can* **102:** 617–642.

Miller, R. R. 1945. A new cyprinid fish from southern Arizona, and Sonora, Mexico, with the description of a new subgenus of *Gila* and a review of related species. *Copeia* **1945** (2): 104–110.

Mori, T. 1928. On the fresh water fishes from the Yalu River, Korea, with descriptions of new species. *J. Chosen Nat. Hist. Soc.* **6:** 1–24.

—— 1930. On the freshwater fishes of the Tumen river, Korea, with descriptions of new species. *J. Chosen Nat. Hist. Soc.* **11:** 1–11.

—— 1934. *The freshwater fishes of Jehol.* Report of the First Scientific Exped. to Manchoukuo. Sect. V, Pt. 1. Waseda Univ. Tokyo. 61 pp.

Nichols, J. T. 1928. Chinese fresh-water fishes in the American Museum of Natural History's collections. *Bull. Amer. Mus. nat. Hist.* **58** (art. 1): 1–62.

Okada, Y. 1960. Studies on the freshwater fishes of Japan II. Special Part. *J. Fac. Fish. pref. Univ. Mie-Tsu* **4** (2): 267–588.

Oliva, O. 1952. A revision of the cyprinid fishes of Czechoslovakia with regard to their secondary sexual characters. *Bulletin International Academie Tcheque de Sciences Prague* **83:** 1–61.

Patterson, C. 1981. The development of the North American fish fauna—a problem of historical biogeography. In: *The evolving biosphere.* Ed. P. L. Forey. British Museum (Nat. Hist.) and Cambridge Univ. Press, London: 265–281.

Rendahl, H. 1928. Beiträge zur Kenntnis der chinesischen Süsswasserfische I. *Ark. Zool.* **20A** (1): 1–193.

Roberts, T. R. 1982 Unculi (horny projections arising from single cells), an adaptive feature of the epidermis of Ostariophysan fishes. *Zool. Scripta* **11** (1): 55–76.

Robins, C. R., Bailey, R. M., Bond, C. E., Brooker, J. R., Lachner, E. A., Lea, R. N. & Scott, W. B. 1980. A list of common and scientific names of fishes from the United States and Canada (4th edition). *American Fisheries Society Special Publication* no. 12: 174 pp.

Sauvage, H. E. 1883. Descriptions de quelques poissons de la collection du Muséum d'Histoire Naturelle. *Bull. Soc. Philom. Paris* **1** (7): 156–161.

—— **& Dabry, deth. P.** 1874. Notes sur les poissons des eaux douces de la Chine. *Ann. Sci. Nat. Zool* **1:** 11.

Scott, W. B. & Crossmann, E. J. 1973. *Freshwater fishes of Canada. Bull. Fish. Res. Board Canada* **184:** 1–966.

Starnes, W. C. & Starnes, L. B. 1978. A new cyprinid of the genus *Phoxinus* endemic to the Upper Cumberland River drainage. *Copeia* **1978** (3): 508–516.

Trewavas, E. 1971. The type-species of the genera *Phoxinellus*, *Pseudophoxinus* and *Paraphoxinus* (Pisces, Cyprinidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **21**(8): 359–361.

Turdakov, F. A. & Piskarev, K. V. 1954. Systematic position of the species *Phoxinus* in the river Chu. *Trudy Inst. Zool. Paras. Kirgiz Acad. Sci.* **2:** 73–77.

Manuscript accepted for publication 17 May 1984

British Museum (Natural History)

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Dr Ethelwynn Trewavas

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Miscellanea

Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

Bulletin of the British Museum (Natural History)

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1. *Acineta* and its morphological relatives

Colin R. Curds

Zoology series Vol 48 No 2 25 April 1985

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The Zoology Series is edited in the Museum's Department of Zoology

Keeper of Zoology : Mr J. F. Peake
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ISBN 0 565 05012 5
ISSN 0007 1498

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Zoology series
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Issued 25 April 1985

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A revision of the Suctoria (Ciliophora, Kinetofragminophora)

1. *Acineta* and its morphological relatives

Colin R. Curds
Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The species of *Acineta* and 7 morphologically related genera have been revised. A new diagnosis for each genus is given with a key to its constituent species. Several genera recently erected by Jankowski (1978) have been synonymised and a new one, *Kellicotta* n. gen., is described. All species are described and figured.

Introduction

The suctoria have received less attention than some of the other ciliate groups. Most papers in the past 50 years have been particularly concerned with the description of the different budding methods found in the group and the inclusion of these data in devising new classifications for the subclass. Keys to their identification have been few and this has led to taxonomic confusion particularly at the generic level. It is apparent that we are still unclear as to what consitutes a genus as far as the suctoria are concerned and this was the first major problem to be overcome. Many difficulties were encountered with the suctoria when preparing a generic key to all freshwater ciliates (Curds, 1982), but it was decided at the time that it was not within the province of that book to include major generic revisions and acceptable published classifications were adhered to as far as possible. The present publication is the first of a series of papers that should enable the ecologist and taxonomist to identify all species of suctoria described to date. The initial approach was to create a database of published information concerning suctorian genera on a computer. An on-line identification programme made it possible to be able to quickly compare the descriptions of species with published generic descriptions, and in this way the accuracy of the original and subsequent generic identifications could be assessed. In a surprising number of cases it was found that species had been assigned to incorrect genera. So far it has been necessary to erect one new genus and several recently described genera have been synonymised. It was

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Bull. Br. Mus. nat. Hist. (Zool.) **48**(2): 75–129 Issued 25 April 1985

strongly felt at the outset that an attempt to check on the identities of all described species of suctoria should be made before any account was written and this stage has now been more or less completed. The database was also used by another programme to automatically generate printed identification keys but these will not be published until a significant proportion of the taxonomic revisionary and descriptive work has been completed since the data are being continually revised as the more detailed aspects of the work progress. It is not intended to publish the series in any particular taxonomic order but rather to concentrate initially on some of the more common, larger and usually taxonomically more difficult genera, along with their nearest morphological relatives. Thus this first part concerns the genus *Acineta* Ehrenberg, 1833 and some closely related genera.

The relative importance of the various characters that have been used for establishing genera have changed considerably over the years. Attributes that were once used as primary characters may now be regarded as unimportant while more recently newer characters, often based on the buds and mode of budding, have been introduced. It was thought therefore that some remarks should be made concerning the characters that have been used as a basis for the revisions included here.

(*a*) *Method of budding.* There are several fundamentally different modes of budding in the suctoria (Batisse, 1975) and the methods have been used in the more recent schemes of classification as one of the primary characters for the diagnosis of families. All of the genera included here rely, or are assumed to rely, upon endogenous bud formation as their method of asexual reproduction. In some cases where the mode of budding has not yet been reported, the inclusion of the species in the genus should only be regarded as provisional. Should the budding method subsequently be reported to be of any other type then the genus or species will need to be transferred to a more appropriate taxon. The number of buds produced has been considered here to have no importance, thus the genus *Acineta* contains some species which produce single buds while others may undergo multiple bud formation.

(*b*) *Ciliation of bud.* Evidence from the literature (Guilcher, 1951) indicates that the ciliation of the bud is of diagnostic importance. For example, all species of the genus *Acineta* have 5–11 oblique ciliary rows while species of the aloricate *Tokophrya*, which have often been confused with *Acineta*, possess 4 transverse ciliary bands. Unfortunately, this information is not often available in original descriptions and more data are urgently needed about the ciliary patterns of suctorian buds.

(*c*) *Tentacles.* The morphology and arrangement of tentacles have been used as taxonomic characters for many years. Early workers soon recognised that different genera tended to have their tentacles arranged in specific ways. For example, some have their tentacles arranged in fascicles, that is, in discrete clumps or bundles while the tentacles of others tended to be more or less equally distributed over all or certain parts of the body. In this revision the presence of fascicles of tentacles and the number of fascicles has been used as a diagnostic character. Jankowski (1967*b*) has recently introduced the term 'actinophore' which Corliss (1979) defines as a 'structure bearing several or a bundle (fascicle) of suctorial tentacles; characteristic of certain suctorians'. Actinophores may be clearly defined arm-like appendages in some genera such as *Stylophrya* and *Stylostoma* where their presence is clearly of some taxonomic value. However, Jankowski (1978) also refers to the presence of actinophores in *Tokophrya quadripartita* which are not at all clearly defined structures but take the form of low conical bulges upon which the tentacles are mounted. In *Acineta* and related genera the actinophores are low lobes of the *Tokophrya* type and in some cases are apparently so reduced as to be completely absent. Thus in the species described here the use of actinophores as a generic character must be regarded as being of little significance.

(*d*) *General morphology.* The presence or absence of a lorica has long been used as a diagnostic character and its use is continued herein. However, while some authorities (Collin, 1912) considered that whether or not the cytoplasmic body completely filled the lorica to be of taxonomic significance here this character is not considered to be important. Lateral flattening of the lorica and body are considered to be of significance and any species in the genus *Acineta* should exhibit lateral compression to some extent. Similarly the aperture in the lorica should also be laterally compressed so that the outline shape should be a dumb-bell slit to oval but never circular.

(*e*) *Attachment.* Most suctoria are attached in some way to a substratum. Attachment is often achieved by the presence of a stalk or in some cases the lorica or cytoplasm is attached directly without an intervening stalk. Two different types of stalk-like structures are recognised in this revision. True stalks are always distinct from the lorica while those which are simply extensions of the lorica (Fig. 1) are not considered to be stalks in the proper sense. The nature of the substratum is not usually considered to be of significance and is certainly not thought to be sufficient grounds alone to erect a separate species and this is also applied to situations where the substrata happen to be different animal species such as crustaceans.

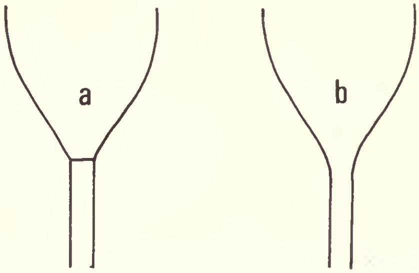


Fig. 1 Two types of attachment organelles found in the Suctoria: (a) stalk; (b) thecostyle, an extension of the lorica.

Genus *ACINETA* Ehrenberg, 1833

A large number of suctorians described to date have, at some time in their nomenclatural history, resided in the genus *Acineta*. Species have been transferred in and out of the genus, often with remarkable rapidity, causing taxonomic chaos and confusion to the biologist who simply wishes to identify a suctorian. Many of these problems arose through the lack of precision used by early taxonomists when defining a genus. However, diagnoses have been emended successively as opinions concerning taxonomically important characters have changed as a result of an increase in knowledge and understanding of the structure and biology of these organisms.

The original diagnosis of the genus was founded.on the description of the species *Acineta tuberosa* Ehrenberg, 1833 and little was added over the next half century. For example, the diagnosis given by Kent (1882) stated that *Acineta* possessed a lorica to which the cytoplasm was either attached or in which it remained freely suspended, it was supported on a rigid stalk and the tentacles were suctorial, capitate and variously distributed. Few significant changes were made until the monographic work of Collin (1912) when he considerably improved precision by the addition of the following criteria: protoplasmic body almost entirely confined in a lorica without a free border, more or less strongly flattened with generally two fascicles of tentacles, reproduction always taking place by means of internal embryos. By this emendment Collin (1912) eliminated some of those species included in the 'first and second groups' of Bütschli (1899) and Sand (1900) which had already been transferred into *Paracineta* Collin, 1911 and the two genera *Periacineta* Collin, 1909 and *Thecacineta* Collin, 1909 respectively. Few changes have been made to Collin's (1912) diagnosis in the intervening years but the generic diagnosis given below adds a little more precision and takes into account some of the new genera recently erected by Jankowski (1978) and the diagnosis given by Curds (1982).

Diagnosis of *Acineta*

Freshwater or marine suctorians whose outline shape varies from oval to triangular. Lorica and

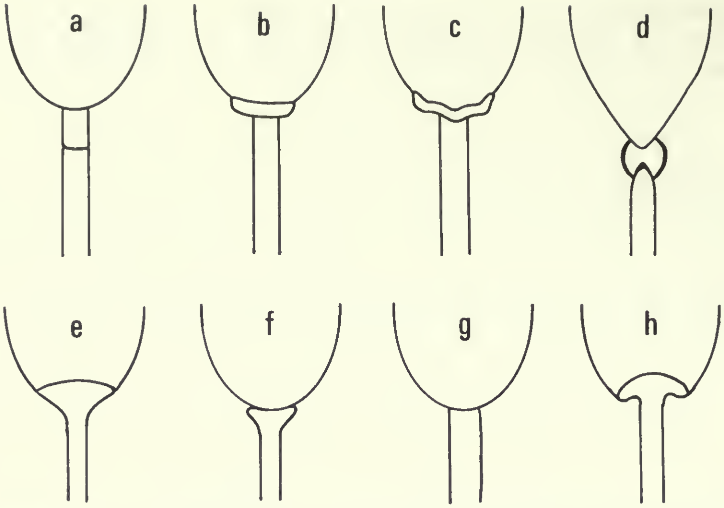


Fig. 2 Various junctions between stalk and lorica found in *Acineta*.

body always laterally compressed, borne upon a stalk and attached to aquatic animals, plants or inanimate objects. Anteriorly, two fascicles of tentacles, arranged in discrete clumps but not rows, project through an apical aperture that is usually dumb-bell shaped but may also be a simple slit or oval shape. Two low lobe-like actinophores usually present each bearing a fascicle of sutorial, capitate tentacles. Reproduction by monogemmic or polygemmic internal budding resulting in the production of ovoid ciliated embryos whose ciliary pattern takes the form of 5–11 transverse to oblique rows.

Key to the species of *Acineta*

1	Stalk joins lorica via a distinct collar (Fig. 2a–d)	2
	Stalk joins lorica without an intervening collar	11
2	Collar about same width as rest of stalk	8
	Collar widens to at least twice stalk width	3
3	Freshwater, attached to Lake Baikal gammarids	4
	Marine	***A. compressa***
4	Collar region a narrow rectangular strip held at right angles to stalk (Fig. 2b)	5
	Collar region curved and/or inserted into posterior depression of lorica	7
5	Stalk much less than length of body whose outline shape is triangular	***A. pulchra***
	Stalk either longer or just shorter than body whose outline is oval to bell-shape	6
6	Edge of lorica scalloped with many rounded cusps, stalk is almost body length	***A. dentata***
	Lorica edge only slightly scalloped if at all, stalk longer than body	***A. lobata***
7	Collar a narrow strip in form of a series of undulating curves (Fig. 2c)	***A. foecunda***
	Collar flared, embedded in depression in lorica	***A. vulgata***
8	Body width approximately equal to body length	***A. compressa***
	Body always longer than its width	9
9	Collar region bulbous (Fig. 2d)	***A. papillifera***
	Collar region not bulbous	10
10	Freshwater	***A. flava***
	Marine	***A. cucullus***
11	Junction of stalk with lorica at least 3 times stalk width and is spatulate (Fig. 2e–h)	12
	Junction of stalk with lorica is less than 3 times stalk width and not spatulate (Fig. 2f–g)	14
12	Spatulate end of stalk embedded in posterior depression in lorica	13
	Spatulate end of stalk not embedded in posterior depression in lorica	***A. pumila***
13	Spatulate end spreads out laterally only (Fig. 2e)	***A. parva***
	Spatulate end spreads out laterally and curves back posteriorly (Fig. 2h)	***A. commensalis***

14	Junction of stalk with lorica cup-like (Fig. 2f)	15
	Stalk sides parallel at junction with lorica (Fig. 2g)	25
15	Freshwater, attached to Baikal gammarids	17
	Marine	16
16	Stalk striated longitudinally, lorica smooth	***A. truncata***
	Stalk smooth, lorica covered with sand grains	***A. shulzi***
17	Several contractile vacuoles present	18
	Single or no contractile vacuoles present	19
18	Tentacles and actinophores able to contract into lorica	***A. tubulifera***
	Actinophores cannot contract into lorica	***A. cordiformis***
19	Actinophores distinctly spherical	***A. sphaerifera***
	Actinophores may be rounded or lobe-like but never distinctly spherical	20
20	Stalk at least 4–5 times body length	***A. cornuta***
	Stalk less than 3 times body length and usually very much less	21
21	Body size small (30–40 µm long)	***A. swarczewskia***
	Body size medium (at least 50 µm long)	22
22	Usually widest at equator, oval outline	***A. ovalis***
	Always widest at apex, conical outline	23
23	Tentacles and cytoplasm confined within lorica	***A. baikalica***
	Tentacles and cytoplasm protrude past lorica rim	24
24	Actinophores anteriorly situated, low lobes	***A. crypturopi***
	Actinophores laterally situated, elongated lobes	***A. biloba***
25	Lorica smooth	26
	Lorica transversely striated, folded, furrowed or ridged	43
26	Freshwater	27
	Marine	36
27	Edge of lorica distinctly scalloped	***A. tulipa***
	Edge of lorica not scalloped	28
28	Stalk long and almost third of greatest width of lorica	***A. pachystylos***
	Stalk usually less than sixth of greatest width of lorica if almost quarter the width then stalk is short	29
29	Lorica wider than long	30
	Lorica longer than wide	32
30	Stalk much shorter than lorica length, nucleus spherical, attached to gammarids	31
	Stalk longer than lorica length, nucleus elongate, attached to aquatic plants	***A. lasanicola***
31	Tentacles not retractile, lorica indistinct, found in Lake Baikal	***A. pugmaea***
	Tentacles retractile, lorica distinct, found in European freshwaters	***A. gammari***
32	Body large (300 µm long), macronucleus curved like a sausage	***A. grandis***
	Body medium–small (less than 100 µm long), macronucleus spherical	33
33	Attached to aquatic plants and inanimate objects	34
	Attached to gammarid crustacea	***A. gammari***
34	Actinophores reduced, contractile vacuole off-centre	***A. simplex***
	Actinophores prominent, contractile vacuole centrally positioned	35
35	Actinophores can retract into lorica	***A. fluviatilis***
	Actinophores cannot retract into lorica	***A. tuberosa***
36	Stalk distinctly longitudinally striated	***A. truncata***
	Stalk not striated longitudinally	37
37	Stalk about same length as lorica	38
	Stalk much shorter than lorica	40
38	Body size large (300 µm long)	***A. calkinsi***
	Body size small–medium (35–100 µm long)	39
39	Lorica oval in outline shape	***A. simplex***
	Lorica triangular in outline shape	***A. tuberosa***
40	Stalk wide (quarter width of body), attached to algae, apparently without tentacles	***A. laevis***
	Stalk thin (less than eighth width of body), attached to crustacea or inanimate objects	41
41	Attached to crustacea	42
	Attached to inanimate objects	***A. tuberosa***
42	Body confined within lorica, only tentacles protrude	***A. crater***
	Body projects out from lorica	***A. corophii***

43 Ectocommensal on crustacea 44
Attached to inanimate objects 47
44 Folds or striations regular, covering most of lorica 45
Folds or striations irregular or restricted to small areas of the lorica 46
45 Posterior end of lorica much wider than stalk . . . . . . ***A. sulcata***
Posterior end of lorica narrows down to stalk width at their junction . . . . ***A. harpacticola***
46 Folds located in posterior half of lorica only, width of lorica almost equal to its length . . . . ***A. branchicola***
Folds and striations irregular, sometimes striated down length of lorica which is longer than wide ***A. karamani***
47 Posterior end of lorica elongated to join stalk, lorica only striated in mid-region . . . ***A. kahli***
Posterior end of lorica broadly rounded, lorica usually striated over entire surface . ***A. tuberosa***

Species descriptions

Acineta tuberosa Ehrenberg, 1833

Brachionus tuberosus Pallas, 1766
Vorticella tuberosa Müller, 1786
Volverella astoma Bory, 1825
Podophrya poculum Allman, 1875 *nomen nudum*
Acineta poculum Hertwig, 1875
Acineta foetida Maupas, 1881
Acineta aequalis Stokes, 1891
Acineta corrugata Stokes, 1894
Acineta sp. Prowasek, 1900
Acineta tuberosa var. *fraiponti* Sand, 1901
Acineta tuberosa var. *foetida* Collin, 1912
Acineta tuberosa f. *brevipes* Collin, 1912
Acineta laomedeae Precht, 1935
Tokophrya species Precht, 1935
Acineta brevicaulis Rieder, 1936
Acineta limnetis Goodrich and Jahn, 1943
Tokophrya microcerberi Delamare Deboutteville and Chappuis, 1956
Acineta tuberosa var. *bipartita* López-Ochoterena, 1963

Description (Figs 3, 4, 5). This the type species small to medium (25–120 µm long), freshwater, brackish or marine loricate suctorian that varies from bell to Y-shape in outline, laterally flattened. Two actinophores present, often well developed but may be reduced in some specimens, each bearing a fascicle of capitate tentacles. Apical aperture dumb-bell shape. Cytoplasm does not always completely fill the lorica which is sometimes smooth but is often transversely striated or ribbed. Stalk variable in length (5–90 µm long) joining lorica without an intervening collar or other structure, usually with basal disc. Attached to a variety of substrata including inanimate objects, aquatic plants, such as *Myriophyllum*, crustacea, such as the shrimp *Crangon*, the isopods *Idothea tricuspidata* and *Microcerberus remyi*, and the amphipod *Gammarus locusta*, also found on the freshwater turtle *Chrysemis picta*. Reproduction by endogenous budding. Oval buds with 5 oblique ciliary rows, incorrectly redrawn with only 4 rows in Kent (1882) see Fig. 3m, n. Spherical macronucleus centrally located, single contractile vacuole situated apically. Often reported from organically polluted environments.

Note. It will be noted from the synonymy list that this species has had a long and rich nomenclatural history. Because it is so variable in almost all of its attributes it has been given many different specific names. It is probably the most commonly reported of all the species in the genus.

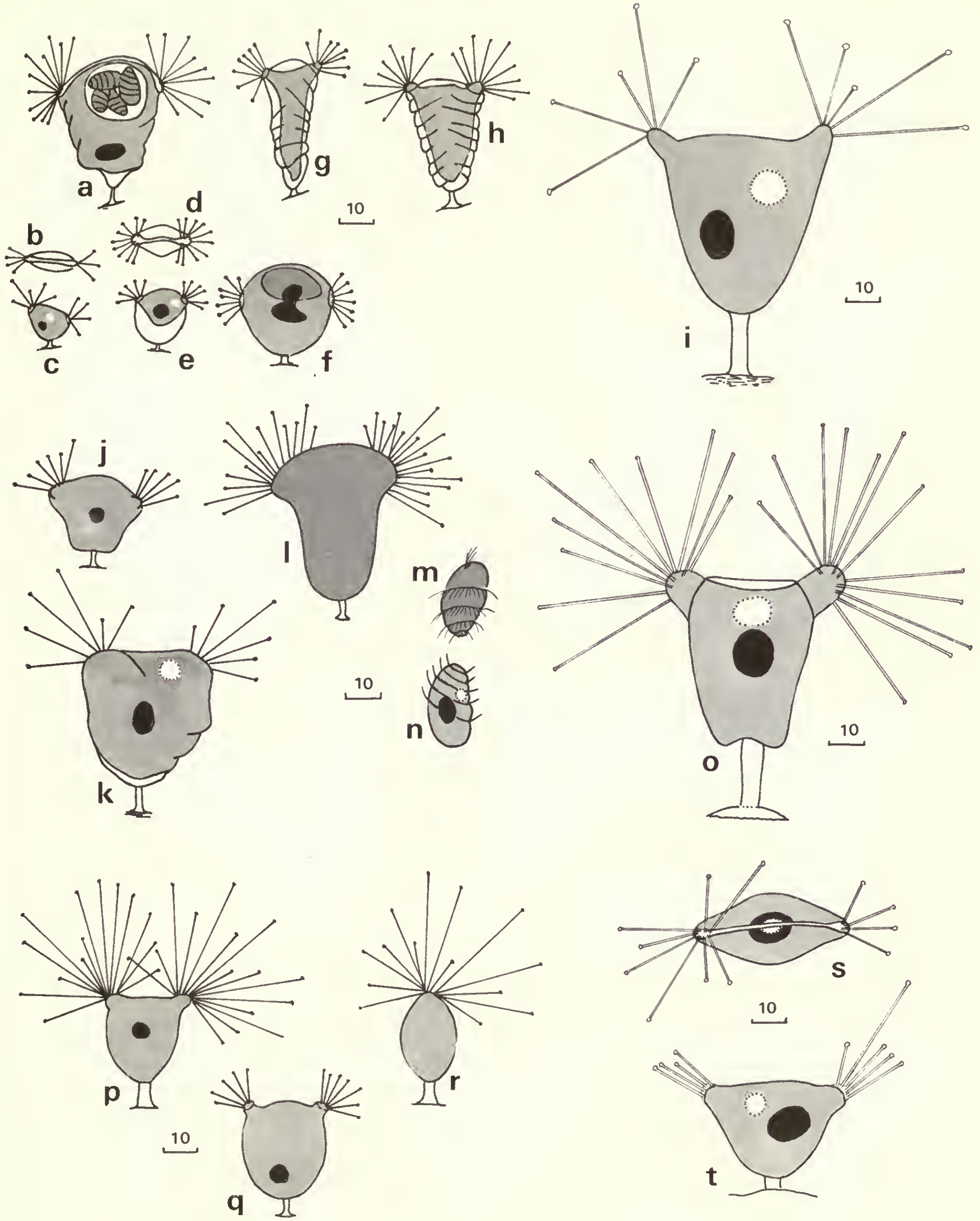
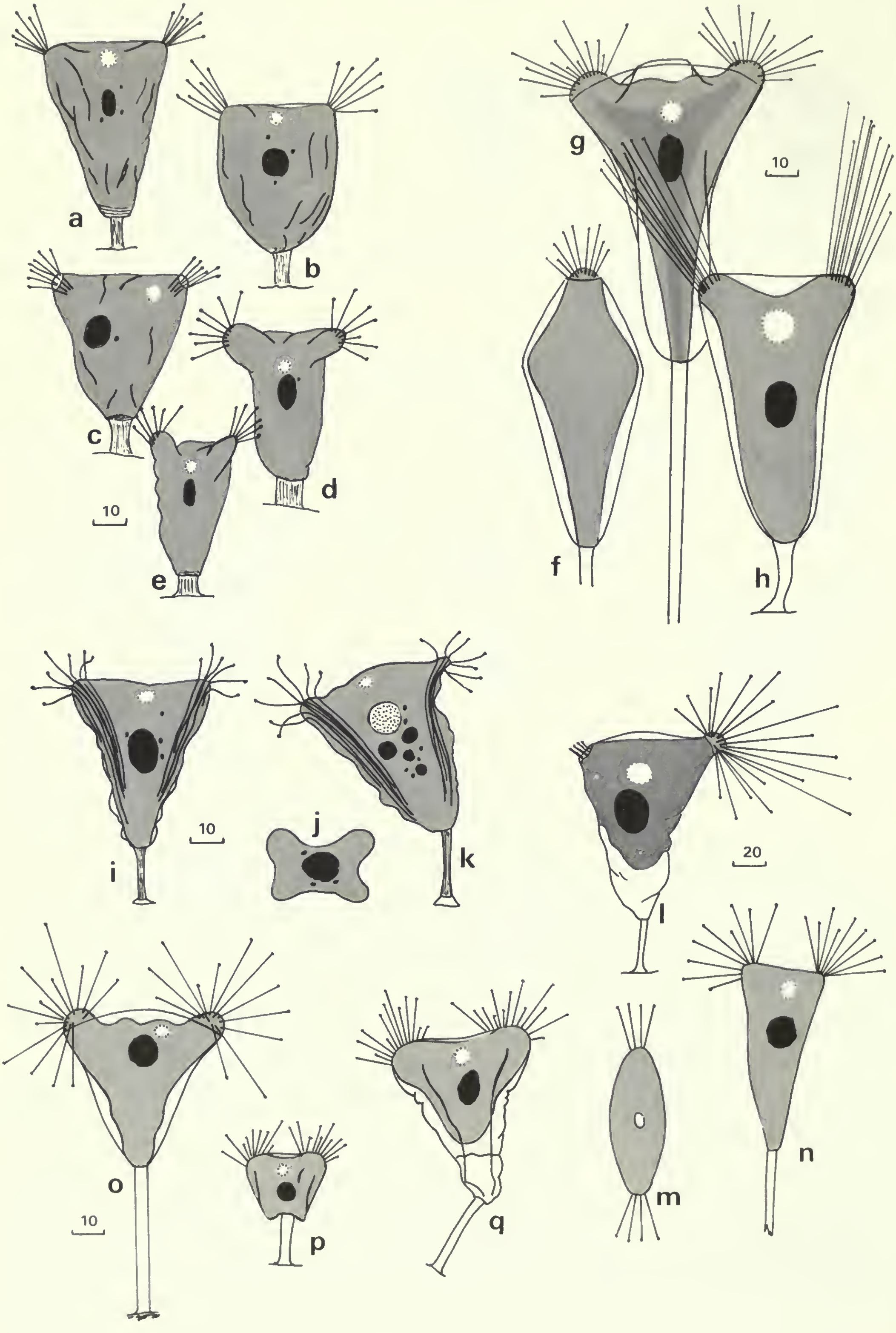


Fig. 3 *Acineta tuberosa:* (a–h) after Maupas, 1881 (called *A. foetida*); (i) after Stokes, 1891 (called *A. aequalis*); (j, l, m) after Collin, 1912 (called *A. tuberosa* var. *foetida*); (k) after Wang & Nie, 1933; (n) ciliated larval form, after Maupas, 1881; (o) after Goodrich & Jahn, 1943 (called *A. limnetis*); (p. r) after Wailes, 1943 (called *A. foetida*); (q) after Gourret & Roeser, 1886 (called *A. foetida*); (s. t) after Rieder, 1936 (called *A. brevicaulis*).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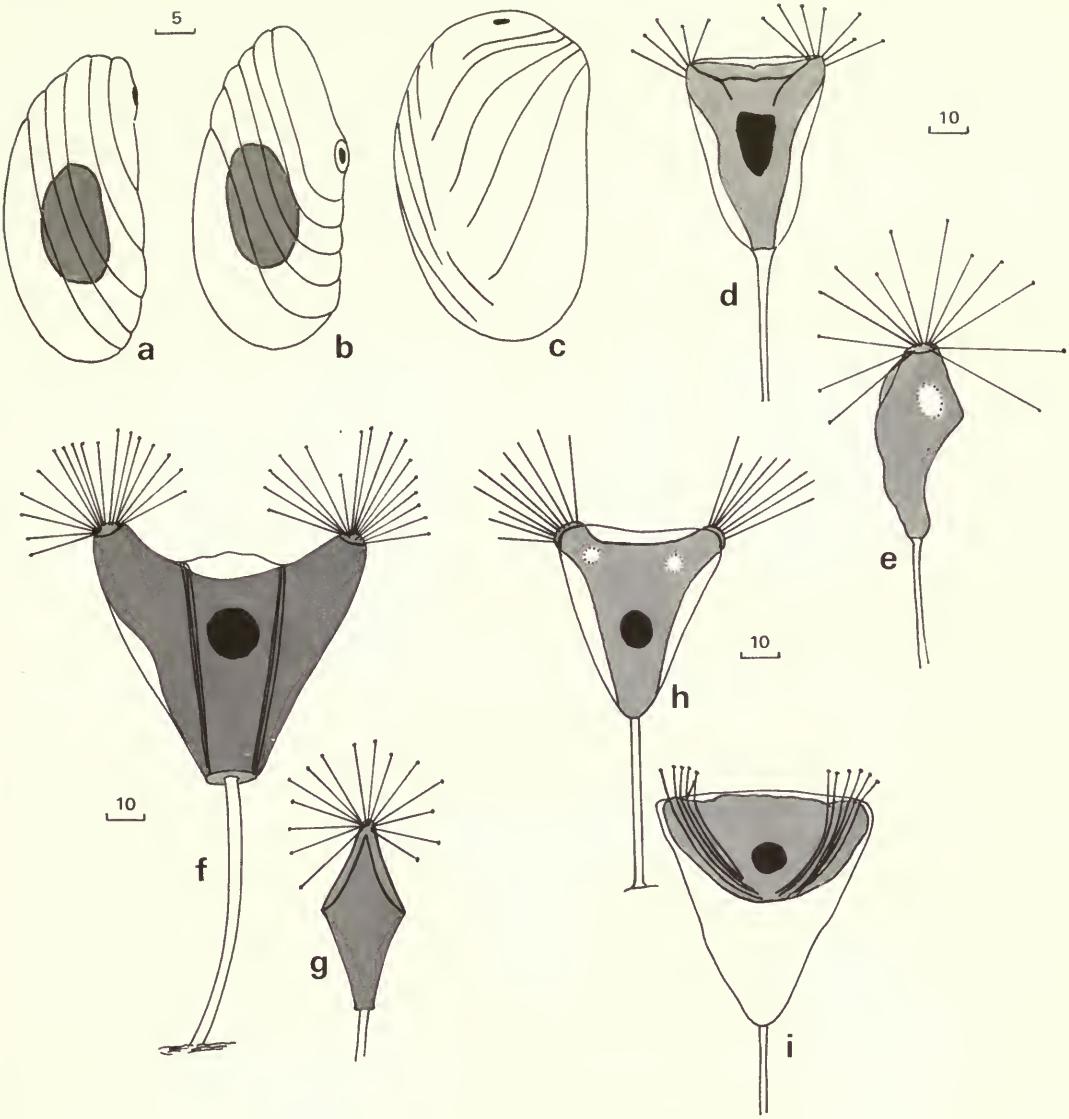

Fig. 5 *Acineta tuberosa*: (a, b) ciliated embryo after Collin, 1912 (called *A. tuberosa* var. *fraiponti*); (c) embryo after Guilcher, 1951; (d, e) after Fraiponti, 1878; (f, g) after Robin, 1879; (h) after Holm, 1925; (i) after Hertwig, 1876 (called *A. poculum*).

Fig. 4 *Acineta tuberosa:* (a–e) after López-Ochoterena, 1963 (a, b called *A. tuberosa* var. *fraiponti* forma *brevipes*; c called *A. tuberosa* var. *foetida*; d, e called *A. tuberosa* var. *bipartita*); (f, g) after Precht, 1935 (called *A. laomedeae*); (h) after Gajewskaja, 1933; (i–k) after Collin, 1912 (called *A. tuberosa* forma *brevipes*); (l) after Collin, 1912 (called *A. tuberosa* var. *foetida*); (m, n) after Wailes, 1943; (o–q) after Precht, 1935 (p. q called *A. foetida*).

Acineta baikalica (Swarczewsky, 1928) n. comb.

Thecacineta baikalica Swarczewsky, 1928
Thecacineta brevistyla Swarczewsky, 1928
Canellana baikalica Jankowski, 1967

DESCRIPTION (Fig. 6). Medium (80–100 µm long), freshwater, loricate species whose outline is an inverted bell shape, strongly compressed laterally. The apical aperture is slit to dumb-bell shaped. Actinophores reduced. Cytoplasm and tentacles confined within the lorica. Stalk short to medium, 10–40 µm, joining the lorica via cup-like expansion in the stalk. Reported from Lake

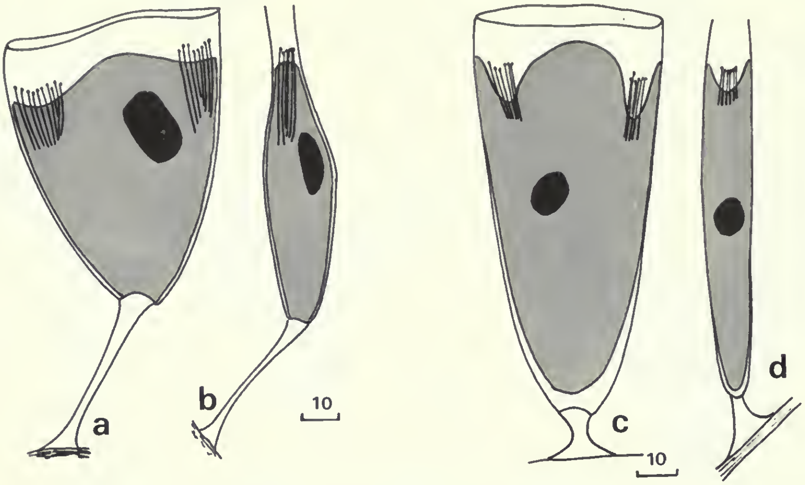

Fig. 6 *Acineta baikalica:* (a, b) after Swarczewsky, 1928 (called *Thecacineta baikalica*); (c, d) Swarczewsky, 1928 (called *Thecacineta brevistyla*).

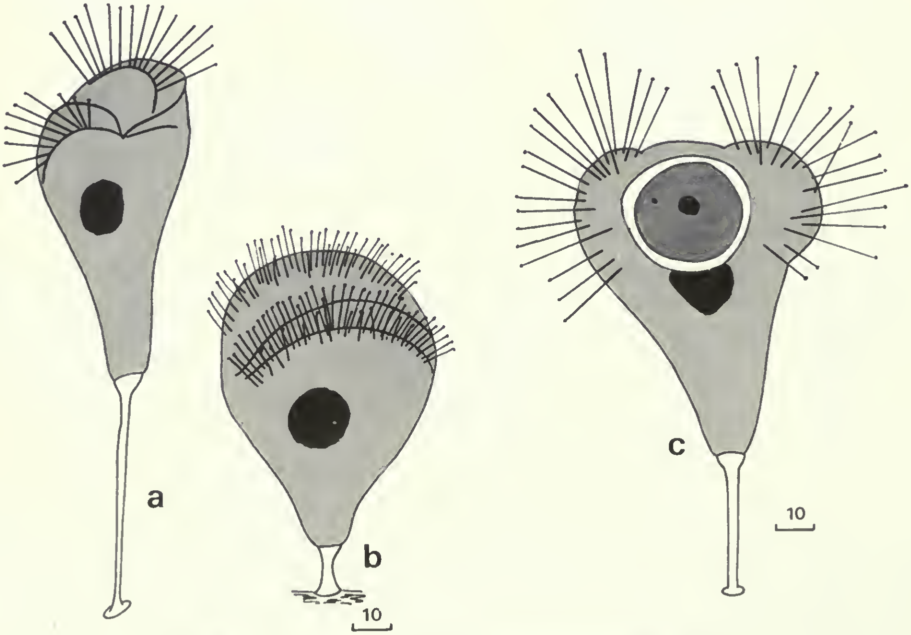

Fig. 7 *Acineta biloba*: (a–c) after Swarczewsky, 1928.

Baikal growing on gammarid crustacea such as *Axelboeckia carpenteri, A. rubra* and *Echinogammarus czerskii.* Reproduction by multiple endogenous budding.

NOTE. Originally two species were described by Swarczewsky (1928) as belonging to the genus *Thecacineta,* however while budding was unknown for one it was known to be endogenous in the other (incorrect for the genus *Thecacineta*). The only real differences between them was the length of the stalk which is not a stable character so they have been merged in this revision. The genus *Canellana* was erected by Jankowski (1967) to include those species with exogenous budding whose bodies were totally confined within the lorica. The latter is not regarded to be a suitable character on which to found a genus since it is known that actinophores can contract down into the lorica in certain species such as *A. fluviatilis* (Penard, 1920) and as stated earlier the budding was originally reported to be endogenous rather than exogenous.

Acineta biloba Swarczewsky, 1928

DESCRIPTION (Fig. 7). Medium (80–90 µm long), freshwater species with conical outline. Body laterally compressed but not strongly so. Two fascicles of capitate tentacles emerge through an oval aperture in the lorica and are borne upon two low but rather wide actinophores. Stalk of variable length, 15–65 µm, but always has a cup-like swelling at the junction between it and the lorica. Reported from Lake Baikal (Swarczewsky, 1928) attached to the gammarid crustacean *Poekilogammarus pictus.* Spherical macronucleus centrally located. Reproduction by multiple endogenous budding.

Acineta branchicola Precht, 1935

DESCRIPTION (Fig. 8). Medium (90–100 µm long), marine species which has an overall conical outline and is strongly laterally compressed. The lorica is distinctly ribbed in the posterior half. Two fascicles of capitate tentacles borne upon lobe-like actinophores which protrude through an apical slit-like aperture in the lorica. Stalk short, 15–20 µm long, with parallel sides at its junction with the lorica. Attached to the gills of the shore crab *Carcinus maenas* and the shrimp *Crangon crangon.* Spherical macronucleus located centrally and there is a single apical contractile vacuole. Reproduction unrecorded.

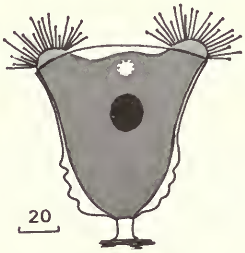

Fig. 8 *Acineta branchicola* after Precht, 1935.

Acineta calkinsi (Calkins, 1902) n. sp.

Acineta tuberosa Calkins, 1902

DESCRIPTION (Fig. 9). Very large (330 µm long), loricate, marine species, with an overall outline conical shape, laterally compressed. Anteriorly there are two large fascicles of distinctly capitate tentacles borne upon lobe-like actinophores which project beyond the slit-like aperture. Stalk 330 µm with parallel sides at its junction with the lorica. Attached to inanimate objects. Spherical macronucleus centrally placed and there is a single apical contractile vacuole.

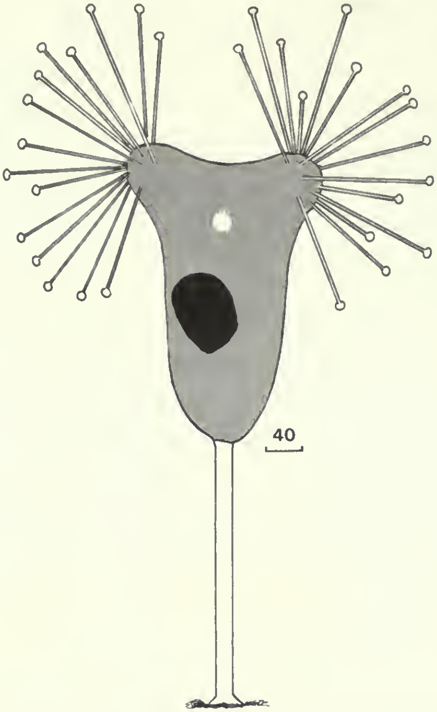

Fig. 9 *Acineta calkinsi*, after Calkins, 1902 (called *A. tuberosa*).

NOTE. Calkins (1902) identified this species as *A. tuberosa*, however the sheer size of this organism along with its possession of very large knobs on the tentacles are thought to be sufficient grounds to create a new species.

Acineta commensalis Swarczewsky, 1928

DESCRIPTION (Fig. 10). Medium (60 µm long), loricate, freshwater species with a pyriform outline. Laterally flattened but not strongly so. There are two fascicles of capitate tentacles

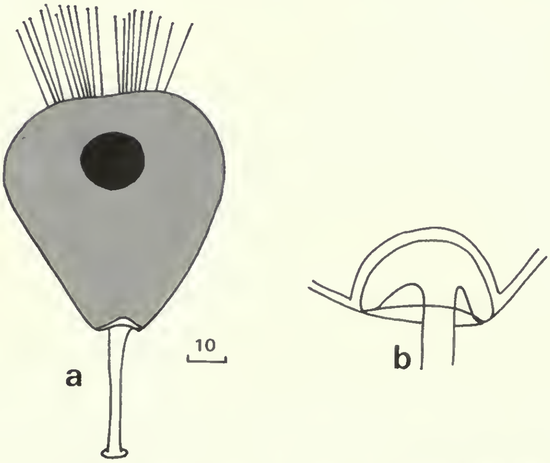

Fig. 10 *Acineta commensalis*, after Swarczewsky, 1928: (a) whole animal; (b) detail of junction between stalk and lorica.

positioned closely together on the apical face of the body. Actinophores indistinct. Stalk medium, 35 µm long, which has a curved spatulate end that is embedded into the posterior end of the lorica. Reported from Lake Baikal attached to the gammarid crustacea *Crypturopus inflatus* and *C. tuberculatus*. There is a spherical macronucleus in the anterior half of the body.

Acineta compressa Claparède and Lachmann, 1859

Cothurnia havniensis Ehrenberg, 1838
Paracineta patula Wailes, 1943

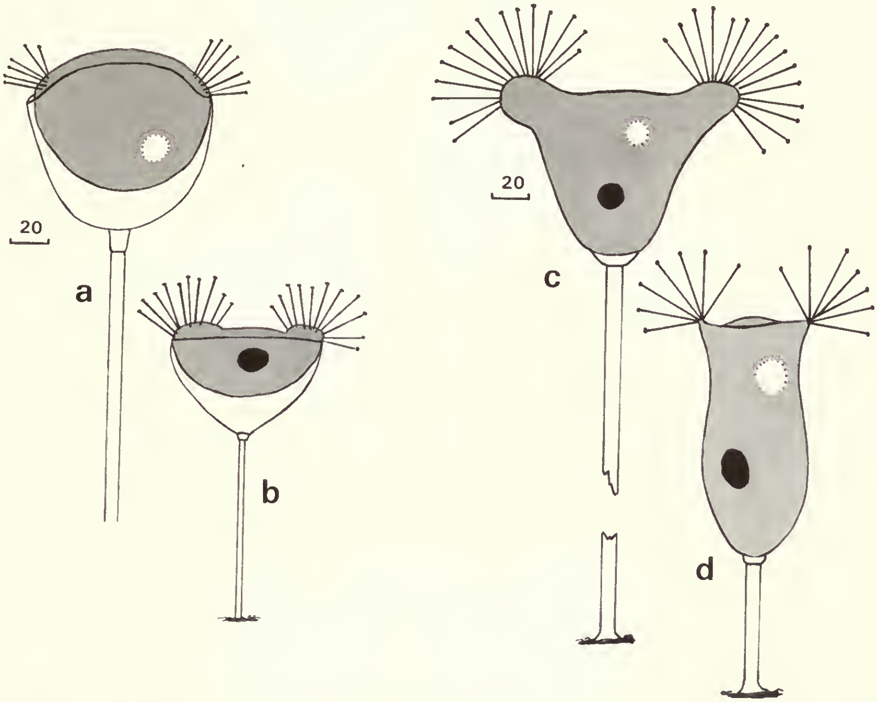

Fig. 11 *Acineta compressa*: (a) after Claparède & Lachmann, 1859; (b) after Wailes, 1943 (called *Paracineta patula*); (c, d) after Wailes, 1943 (called *A. tuberosa*).

Description (Fig. 11). Medium (60–130 µm long), marine, loricate species that is oval to conical in outline, usually as broad or broader than deep, strongly flattened laterally. There are two anterior–lateral actinophores each bearing a fascicle of capitate tentacles. Stalk long, 100–250 µm, which joins the lorica via a definite collar-like region. Found attached to marine algae. Spherical macronucleus and a single contractile vacuole.

Note. Collin (1912) considered *Acineta papillifera* Keppen, 1888 to be a synonym of this species. Kahl (1934) disagreed and reinstated *A. papillifera* whose stalk collar has a more complicated structure than *A. compressa*.

Acineta cordiformis Swarczewsky, 1928

Description (Fig. 12). Medium (100–120 µm long) freshwater, loricate species whose outline appearance is almost a V-shape. This unusual shape is due to the presence of two rather long rounded anterior–lateral actinophores. Laterally flattened. Actinophores project well beyond the lorica rim each bearing a fascicle of capitate tentacles. Stalk long, 200 µm, and joins the lorica via a cup-like expansion of its end. Reported from Lake Baikal attached to the gammarid crustacea *Acanthogammarus albus, A. maximus, A. godlewskii, Garjajewia cabanisi* and *G. zienkowiczi.*

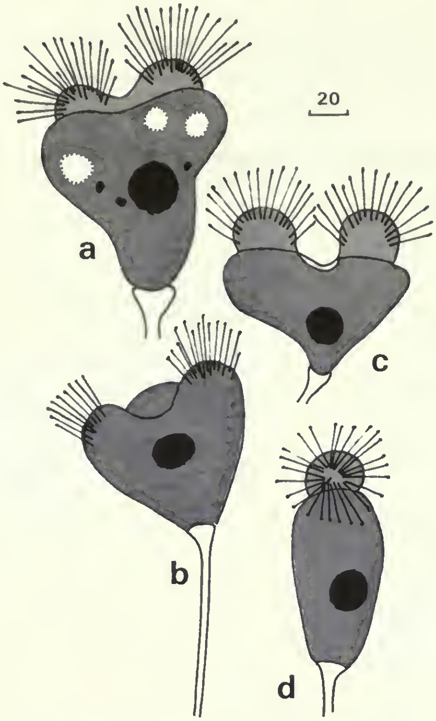

Fig. 12 *Acineta cordiformis*, after Swarczewsky, 1928.

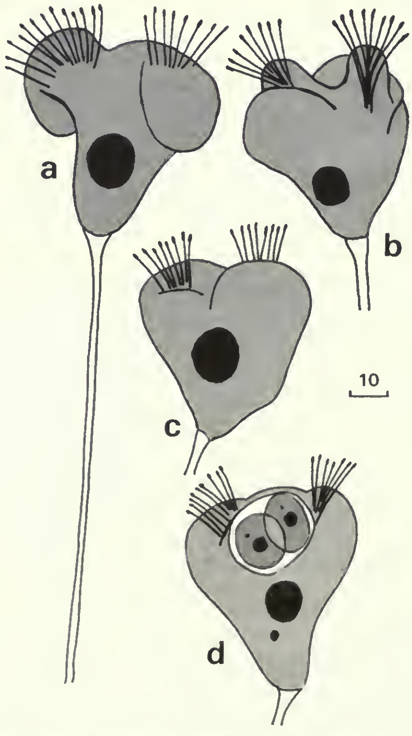

Fig. 13 *Acineta cornuta*, after Swarczewsky, 1928.

There may be several contractile vacuoles in the anterior body half and a single spherical macronucleus. Reproduction by monogemmic endogenous budding.

Acineta cornuta Swarczewsky, 1928

Description (Fig. 13). Medium (50–60 µm long), freshwater, loricate suctorian that is distinctly pear-shaped in outline, weakly compressed laterally. The two actinophores are well defined being rounded lobes on either side of the anterior face each bearing a fascicle of capitate tentacles. Stalk long, 120 µm, joining the base of the lorica via a cup-like expansion. Reported from Lake Baikal where it is found attached to many species of gammarid crustacea including, *Abissogammarus petersi, A. semenkewitschi, A. swarczewsky, A. sarmatus, Odonthogammarus calcaratus, Parapallasea borowskii, Ommatogammarus carneolus, O. albinus* and *Echinogammarus ussolzewi.* There is a single spherical macronucleus and reproduction is by multiple endogenous budding.

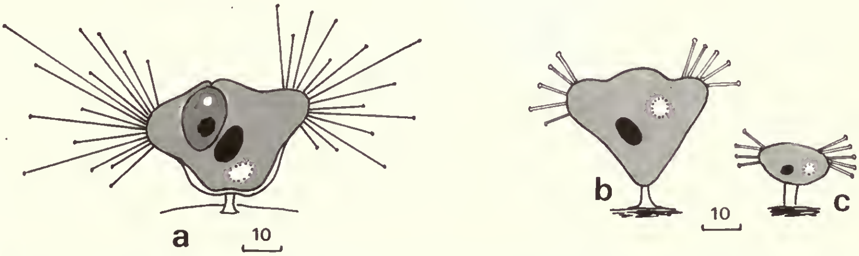

Fig. 14 *Acineta corophii*: (a) after Collin, 1912; (b, c) after Wailes, 1943 (called *A. minuta*).

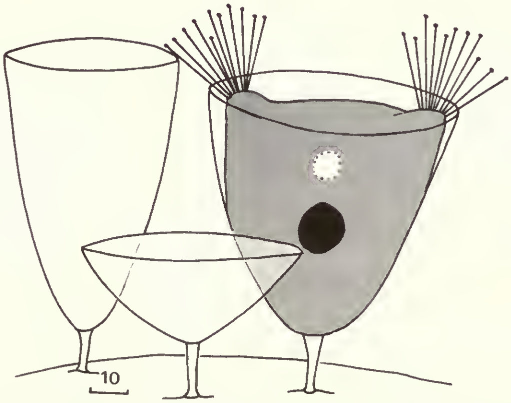

Fig. 15 *Acineta crater*, after Gajewskaja, 1933 (called *Thecacineta crater*).

Acineta corophii Collin, 1912

Acineta minuta Wailes, 1928

Description (Fig. 14). Small (15–30 µm long), marine, loricate suctorian, oval to triangular in outline and always wider than deep. Laterally flattened. Anteriorly the two lobe-like actinophores project well out beyond the rim of the lorica, each bearing a fascicle of capitate tentacles. Stalk short, 5–10 µm, with a basal disc, attached to crustacea such as copepods and to the branchial lamellae of *Corophium longicorne*. There is a single ovoid macronucleus and a contractile vacuole. Reproduction is by monogemmic endogenous budding.

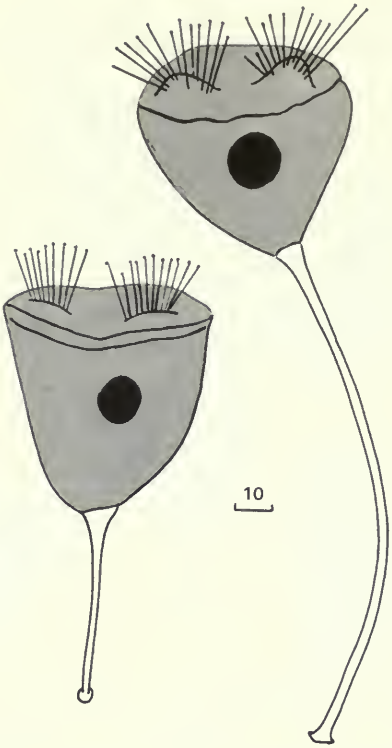

Fig. 16 *Acineta crypturopi,* after Swarczewsky, 1928.

Acineta crater (Gajewskaja, 1933) Matthes, 1956

Thecacineta crater Gajewskaja, 1933

Description (Fig. 15). Medium (70–80 μm long), marine suctorian that inhabits a laterally flattened cup to wine glass shaped lorica. Actinophores present but indistinct, each bearing a fascicle of capitate tentacles that protrude through the oval aperture in the lorica. Stalk short, about 15 μm, attached to gammarid crustacea. There is a single spherical macronucleus centrally located and a contractile vacuole situated in the anterior body half. Reproduction unrecorded.

Acineta crypturopi Swarczewsky, 1928

Description (Fig. 16). Medium (50–60 μm long), freshwater, loricate suctorian that has a cup or bell to pyriform outline. Lateral compression weak. The apical face of the body flattened with two low lobe-like actinophores each bearing the bunches of capitate tentacles. Aperture of lorica oval in outline. Stalk long, 50–140 μm, with a cup-like swelling at its junction with the lorica. Reported from Lake Baikal attached to the gammarid crustacea *Crypturopus pachytus* and *C. inflatus.* There is a single, centrally located, spherical macronucleus. Reproduction unrecorded.

Acineta cucullus Claparède and Lachmann, 1859

Description (Fig. 17). Large (260 μm long), marine, suctorian that inhabits a weakly flattened, wine-glass shaped lorica. The lorica aperture is oval in outline but apparently there is a large semi-circular notch in one of its sides. Actinophores reduced. Two fascicles of capitate tentacles. Stalk at least length of body, joining the lorica via a distinct but simple collar-like region. Attached to the marine alga *Zostera.* Reproduction by multiple endogenous budding resulting in oval buds bearing 'many' transverse rows of cilia. Each bud contains a contractile vacuole.

Note. Collin (1912) considered this species to be synonymous with *Acineta tuberosa,* however later Kahl (1934) reinstated it as a species in its own right. The present author considers that the

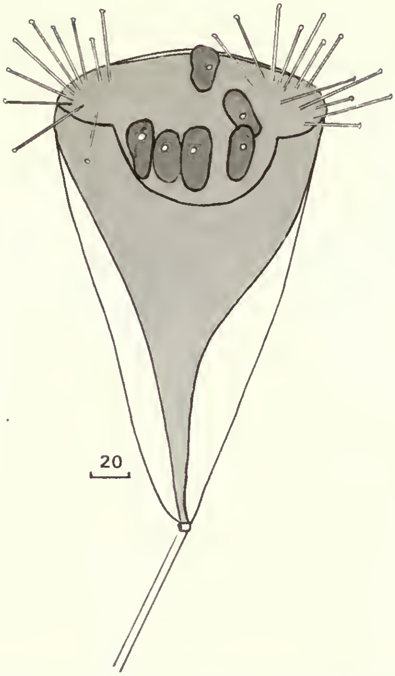

Fig. 17 *Acineta cucullus,* after Claparède & Lachmann, 1859.

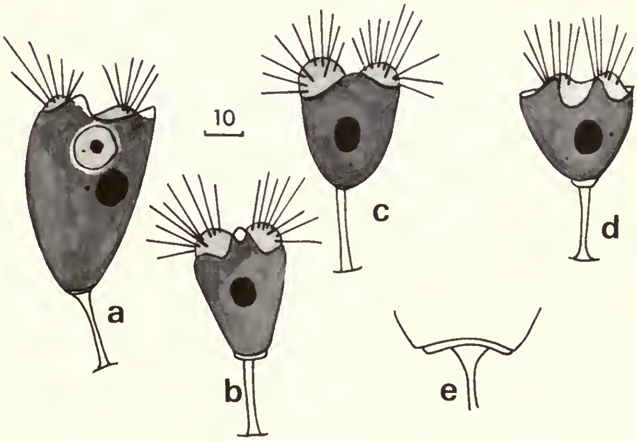

Fig. 18 *Acineta dentata,* after Swarczewsky, 1928.

presence of a collar at the junction of stalk and the deep semi-circular notch in the lorica rim are sufficient to retain this as a distinct species.

Acineta dentata (Swarczewsky, 1928) n.comb.

Thecacineta dentata Swarczewsky, 1928

Description (Fig. 18). Small (30–50 µm long), loricate, freshwater species that is bell-shape in outline. The edge of the apical aperture is strongly scalloped to form several prominent rounded projections. Two actinophores protrude from the lorica, each bearing a fascicle of tentacles. Stalk less than lorica length, joining the latter via a collar-like strip that is at least twice the stalk width. Reported from Lake Baikal attached to the gammarid crustacea *Odonthogammarus improvisus* and *O. korotneffi*. Macronucleus oval, reproduction by single oval endogenous buds.

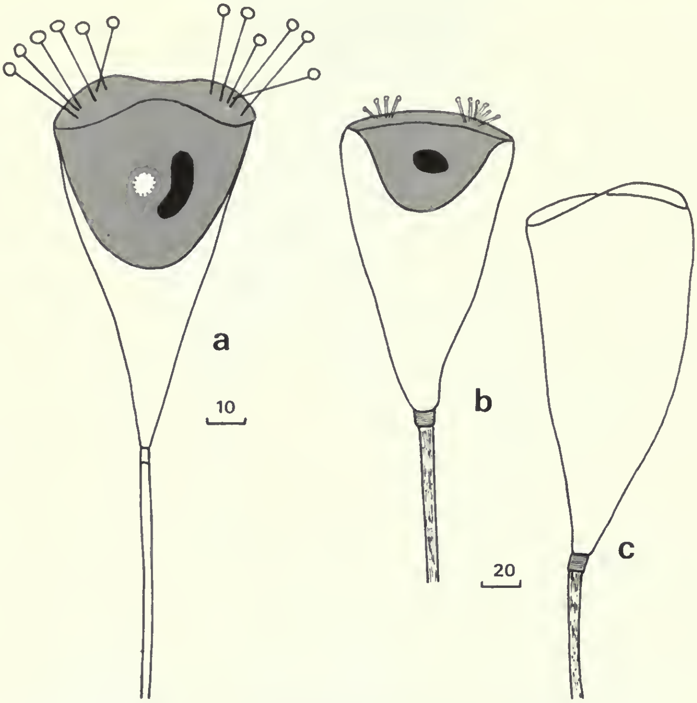

Fig. 19 *Acineta flava*, after Kellicott, 1885.

Acineta flava Kellicott, 1885

Acineta maxima Rieder, 1936

Description (Fig. 19). Large (100–200 µm long), freshwater, loricate species that is conical in shape with lateral compression. The body does not completely fill the lorica and occupies only the anterior half. The lorica aperture is a dumb-bell shaped slit through which the two fascicles of capitate tentacles protrude. Actinophores reduced. Stalk at least equal to the body length, with a simple collar region at its junction with the lorica. There is a basal disc, found attached to organic debris and the green alga *Cladophora glomerata*. Macronucleus spherical to ovoid, located centrally with the contractile vacuole. Reproduction unrecorded.

Acineta fluviatilis Stokes, 1885

Description (Fig. 20). Medium (65 µm long) sized, freshwater, loricate species that is pyriform to triangular in outline, strongly compressed laterally. The apical aperture is slit-like through which the two fascicles borne upon lobe-like actinophores protrude. Actinophores independently contractile. Stalk of variable length, 20–90 µm, joining the lorica without any collar or cup-like region. Attached to the aquatic plant *Vallisneria spiralis*. With centrally located spherical macronucleus and apical contractile vacuole. Reproduction described by Penard (1920) as monogemmic endogenous budding.

Note. Originally described by Stokes (1885*b*).

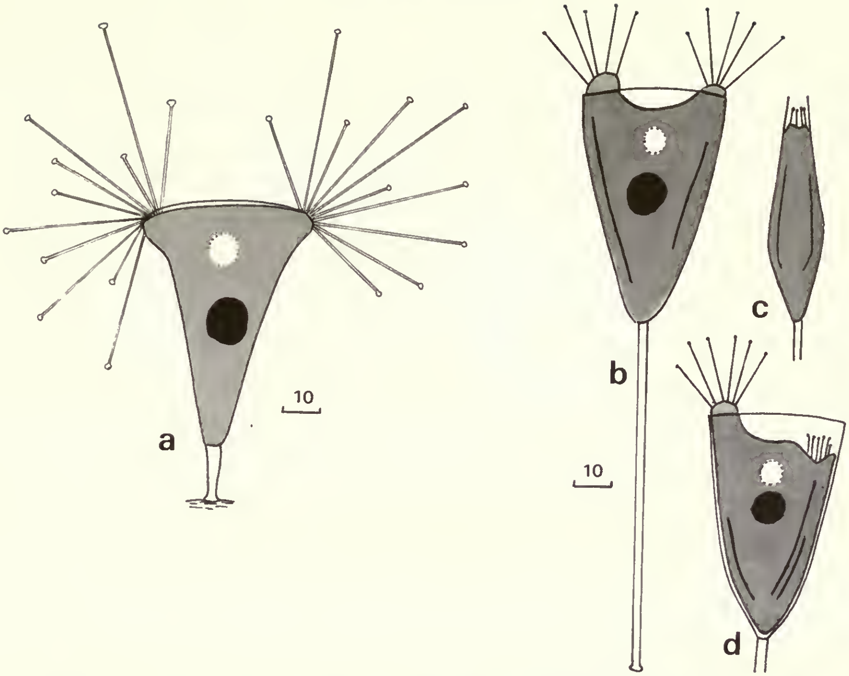

Fig. 20 *Acineta fluviatilis*: (a) after Stokes, 1885*b*; (b) after Penard, 1920.

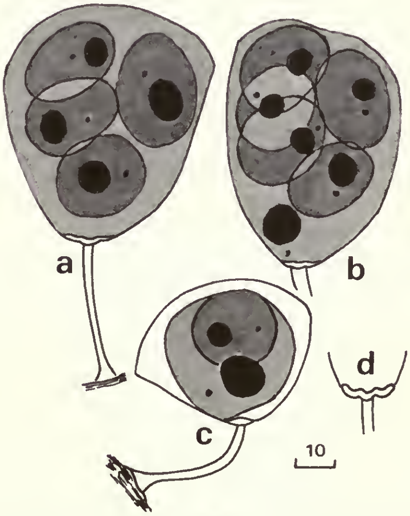

Fig. 21 *Acineta foecunda*, after Swarczewsky, 1928; (a–c) whole animals showing buds; (d) detail of junction of stalk and lorica.

Acineta foecunda Swarczewsky, 1928

Description (Fig. 21). Small to medium (40–65 μm long), freshwater, loricate suctorian whose outline is oval to bell shape, laterally flattened. The apical aperture is oval. Actinophores reduced to lateral flaps on which the short capitate tentacles are mounted. The stalk, which is approximately the same length as the body, joins the lorica via a curved, wave-like strip, collar

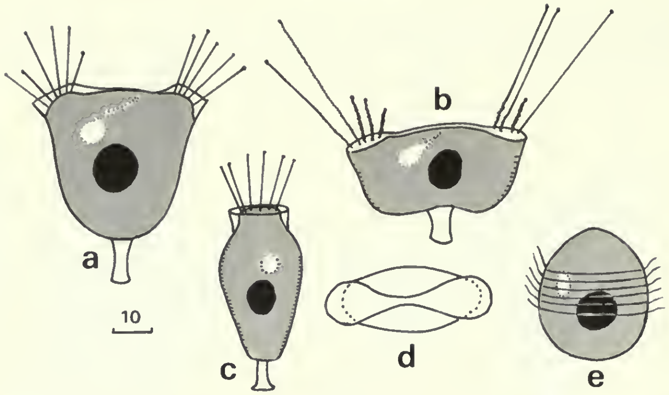

Fig. 22 *Acineta gammari*, after Penard, 1920 (called *Periacineta gammari*); (a, b) lateral view; (c, d) end and top views respectively; (e) ciliated larva.

region. Reported from Lake Baikal attached to the gammarid crustacean *Cryturopus pachytus*. Reproduction by multiple endogenous budding producing 2–5 buds at a time.

Acineta gammari (Penard, 1920) Matthes, 1954

Periacineta gammari Penard, 1920

Description (Fig. 22). Small (40 µm long), freshwater, loricate suctorian species whose outline is an inverted bell-shape, laterally flattened. The apical aperture is dumb-bell shaped through which the two fascicles of capitate tentacles protrude. Tentacles retractile. Actinophores reduced to small bumps confined within the limits of the lorica. The stalk is short (10 µm long) and has parallel sides for its complete length. Found on *Gammarus pulex* where it was feeding on the ciliate *Larvulina*. Reproduction by monogemmic endogenous budding producing ovoid buds with six transverse ciliary bands. Spherical macronucleus and single apical contractile vacuole with a canal.

Note. Although Penard (1920) realised that this species appeared to be an *Acineta* he was convinced that in reality it belonged to the genus *Periacineta*. The latter genus has now no taxonomic status since Matthes (1954) transferred the type species to another genus. The general morphology along with the ciliation of the embryo are certainly sufficient grounds to include this species in the genus *Acineta*.

Acineta grandis Kent, 1881

Description (Fig. 23). Large (320 µm long), freshwater, loricate suctorian whose outline is that of an inverted bell-shape, laterally flattened. The apical aperture is dumb-bell shape and the two low actinophores each bearing a fascicle of capitate tentacles just protrude beyond its rim. Cytoplasm does not always completely fill the lorica but often is confined to the anterior half. The stalk is up to 1500 µm long with parallel sides and attached to aquatic plants such as *Anacharis*, *Nitella* and *Potamogeton*. Macronucleus elongate in the form of a sausage, large central contractile vacuole.

Acineta harpacticola Precht, 1935

Description (Fig. 24). Medium to large (120 µm long) marine, loricate species whose lorica is almost completely covered in transverse ribs or ridges. The lorica is laterally flattened and there is a dumb-bell shaped apical aperture through which the two lobe-like actinophores bearing

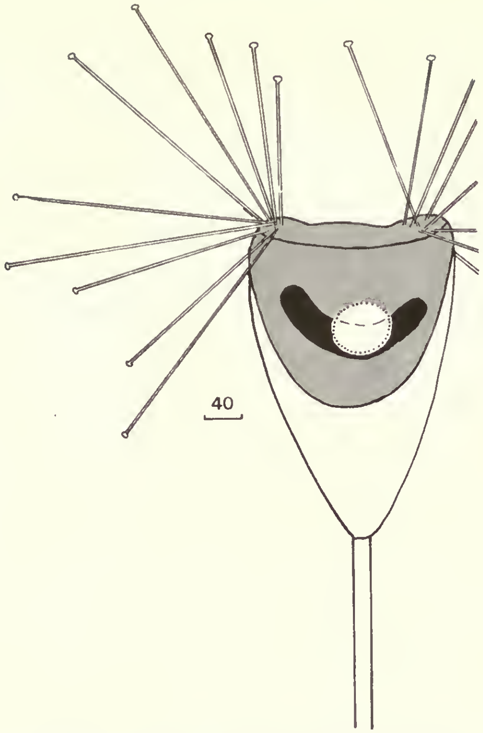

Fig. 23 *Acineta grandis*, after Kent, 1881.

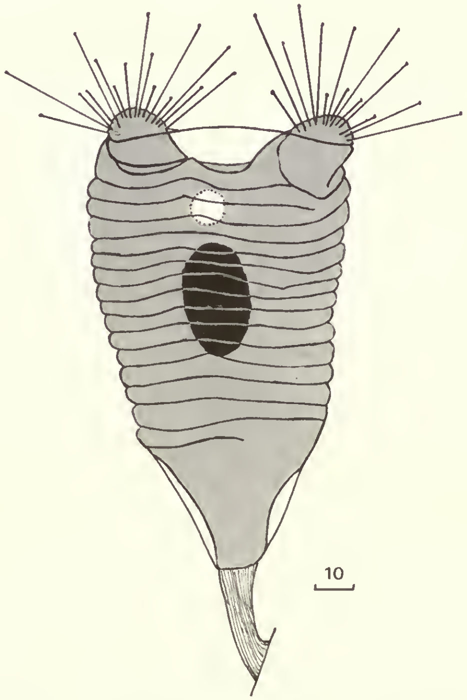

Fig. 24 *Acineta harpacticola*, after Precht, 1935.

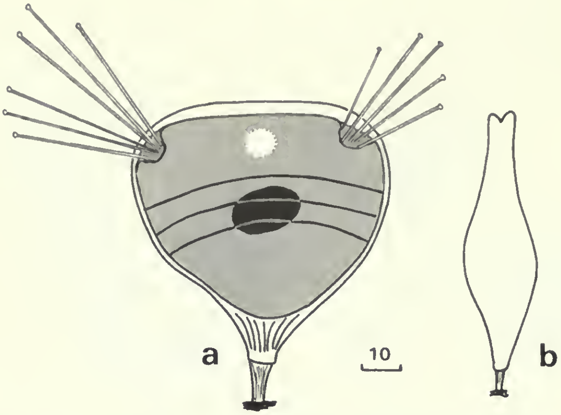

Fig. 25 *Acineta kahli,* after Kahl, 1934 (called *A. pulchra*).

capitate tentacles emerge. Stalk short, 25–30 µm long, attached to the hapacticoid copepod *Laomedea*. Ovoid macronucleus centrally located, with single apical contractile vacuole.

Acineta kahli (Kahl, 1934) nom. nov.

Acineta pulchra Kahl, 1934 not *A. pulchra* Swarczewsky, 1928

DESCRIPTION (Fig. 25). Medium (70 µm long), marine, loricate species with a pyriform outline, laterally flattened. The lorica is strongly transversely striated in the equatorial region. Actinophores reduced. Two fascicles of capitate tentacles which project through the apical slit-like aperture. Stalk short, 10 µm long, attached to inanimate objects. Ovoid central macronucleus present and an apical contractile vacuole. Reproduction undescribed.

NOTE. When Kahl (1934) first described this species the specific name *pulchra* was preoccupied by *Acineta pulchra* Swarczewsky, 1928. In view of this the organism has here been assigned the replacement name *kahli*.

Acineta karamani Hadži, 1940

DESCRIPTION (Fig. 26). Medium to large (40–150 µm long), marine, loricate suctorian whose outline varies from oval to triangular to almost Y-shaped, flattened laterally. The apical aperture in the lorica is the typical dumb-bell shape through which the two fascicles of capitate tentacles protrude. Actinophores lobe-like usually well developed but can be reduced on some occasions. Cytoplasm does not completely fill the lorica in a fully grown specimen and the posterior quarter of the lorica is usually empty. Lorica may be striated either longitudinally and/or transversely. The stalk is short, 10 µm long and attached to the shrimp *Atyaephrya desmaresti*. Macronucleus ovoid to irregular in shape, there may be two apical contractile vacuoles present.

Acineta laevis Dons, 1918

DESCRIPTION (Fig. 27). Small (40 µm long), loricate, marine species that has apparently lost its tentacles or perhaps represents a resting stage. Lorica cup-like to oval in outline, laterally compressed. Stalk short, 10 µm long, but wide, 8 µm, attached to red algae. Actinophores reduced. Single contractile vacuole.

NOTE. This species has been described on two occasions (Dons, 1918; Wailes, 1943) and neither author observed the presence of tentacles.

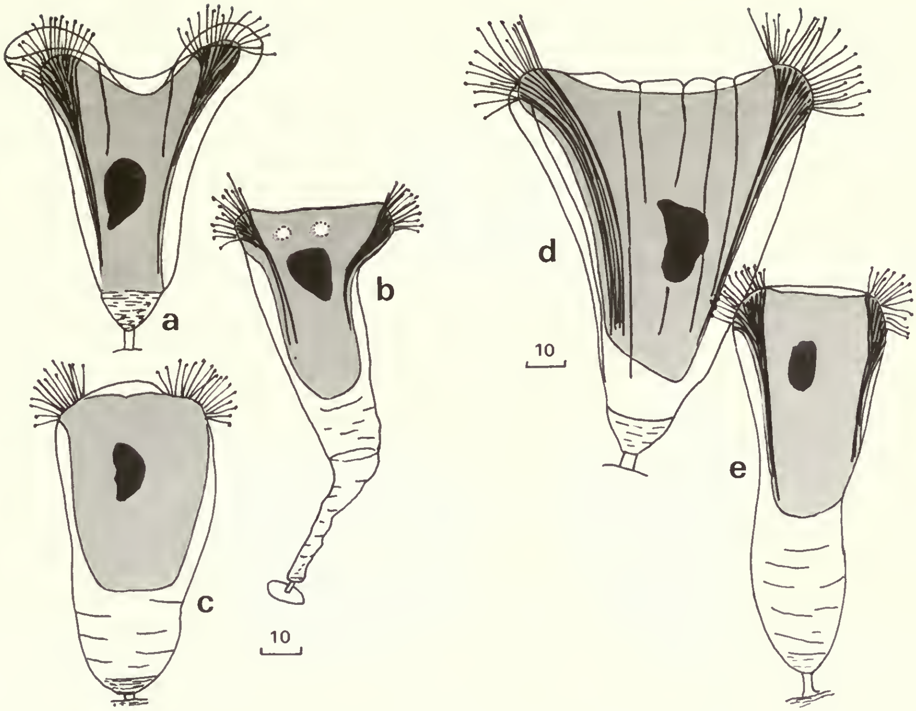

Fig. 26 *Acineta karamani,* after Hadži, 1940.

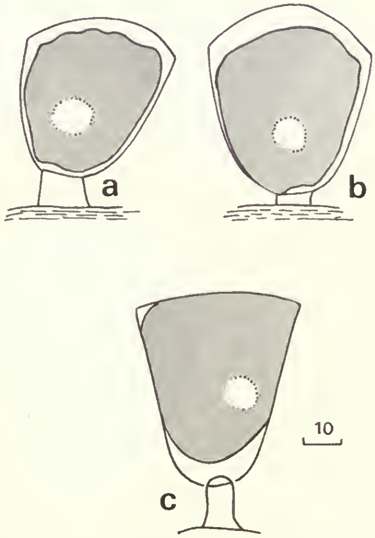

Fig. 27 *Acineta laevis*: (a, b) after Dons, 1918; (c) after Wailes, 1943.

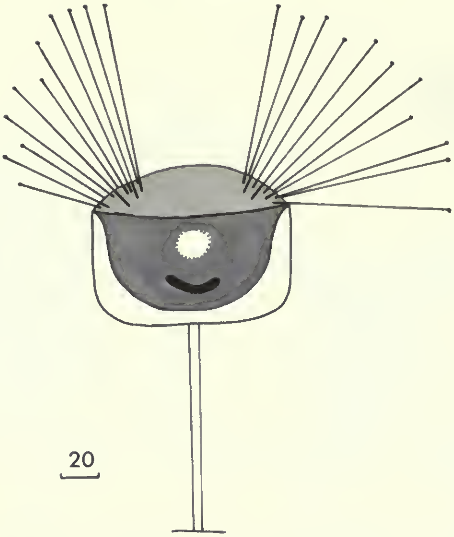

Fig. 28 *Acineta lasanicola*, after Maskell, 1887.

Acineta lasanicola Maskell, 1887

DESCRIPTION (Fig. 28). Medium (55 µm long), freshwater, loricate species whose lorica is broader than deep, looking rather like a saucepan. Actinophores reduced but the cytoplasm extends beyond the oval apical aperture to form a rounded dome. Two fascicles of capitate tentacles present. Stalk twice the length of the lorica. Contractile vacuole centrally located. Macronucleus elongate, curved like a sausage. Reported from New Zealand.

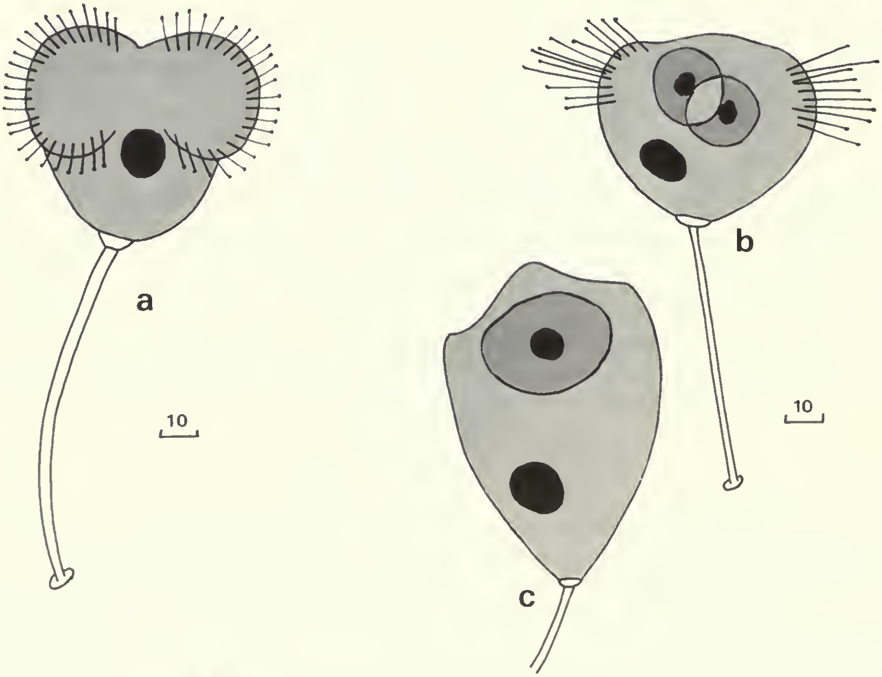

Fig. 29 *Acineta lobata*, after Swarczewsky, 1928.

Acineta lobata Swarczewsky, 1928

Description (Fig. 29). Medium (50–90 µm long), freshwater, loricate species that is oval to pyriform in outline, laterally compressed but not strongly so. Apical aperture broadly dumb-bell shaped. Two large rounded lobe-like actinophores present, each bearing a fascicle of capitate tentacles which project out through the aperture. Stalk long, 80–100 µm, and joins the lorica via a broad collar region. Reported from Lake Baikal attached to the gammarid crustacean *Odonthogammarus pulcherrimus*. Centrally located spherical macronucleus present, reproduction by multiple endogenous budding.

Acineta ovalis Swarczewsky, 1928

Description (Fig. 30). Medium (60 µm long), freshwater, loricate suctorian that is oval in outline, wider than long, lateral compression weak. There is an oval apical aperture through

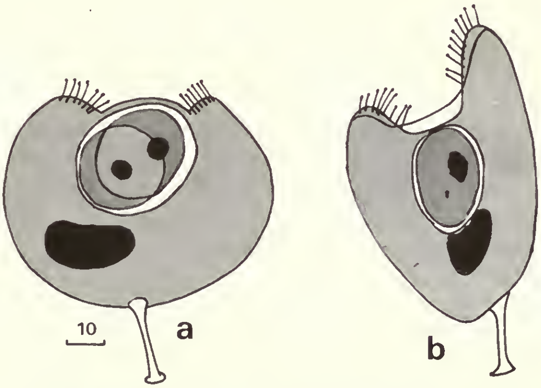

Fig. 30 *Acineta ovalis*, after Swarczewsky, 1928.

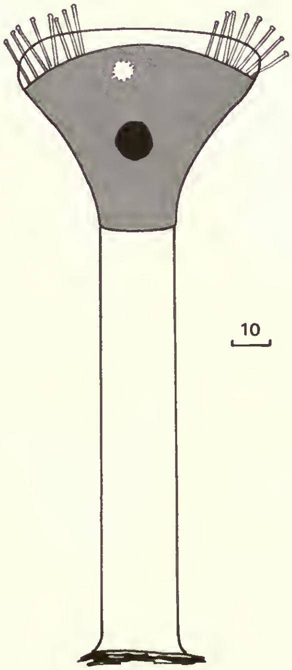

Fig. 31 *Acineta pachystylos* after Holm, 1925 (called *Thecacineta pachystylos*).

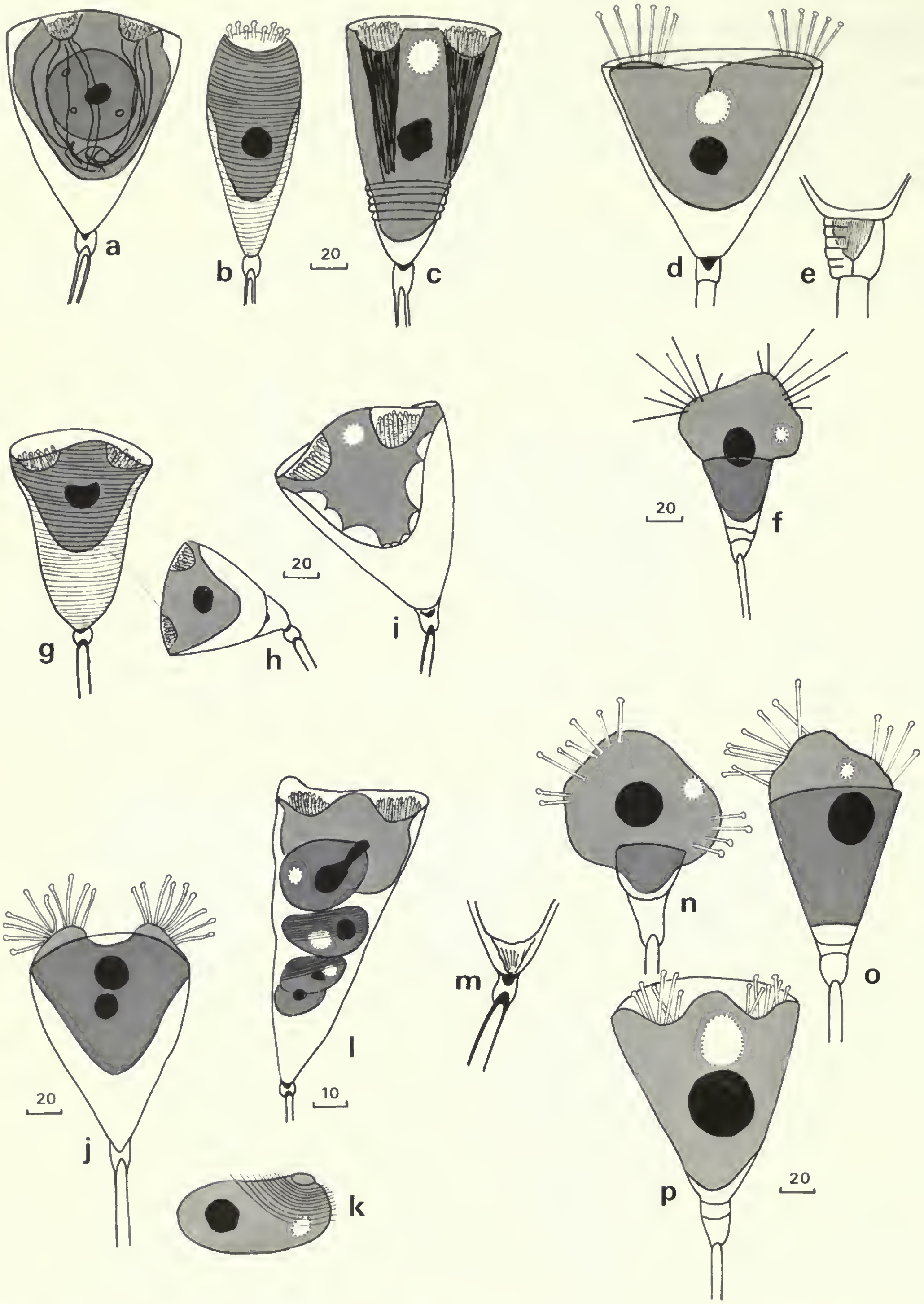
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Fig. 32 *Acineta papillifera*: (a–c) after Collin, 1912; (d, e) after Penard, 1920; (f) after Holm, 1925; (g–i) after Collin, 1912; (j, k) after Keppen, 1888; (l, m) after Collin, 1912; (n–p) after Keppen, 1888.

which the two fascicles of short capitate tentacles just protrude. Actinophores lobe-like. Stalk medium length, 20 µm, joining lorica via a cup-like expansion. Reported from Lake Baikal attached to the gammarid crustacean *Poekilogammarus sukaczewi.* Macronucleus ovoid, reproduction by multiple endogenous budding.

Acineta pachystylos (Holm, 1925) Matthes, 1956

Thecacineta pachystylos Holm, 1925

Description (Fig. 31). Small to medium (50 µm long), freshwater, loricate suctorian that is almost triangular in outline, laterally flattened. The apical aperture is slit-like through which the two fascicles of capitate tentacles just protrude. Cytoplasm confined well within the lorica, actinophores reduced. Stalk long, 110 µm, and exceptionally wide, 20 µm, with parallel sides at junction with lorica. Attached to inanimate objects. Macronucleus spherical, with single apical contractile vacuole. Reproduction not described.

Acineta papillifera Keppen, 1888

Acineta collini Kahl, 1934
Acinetella collini Jankowski, 1978

Description (Fig. 32). Medium to large (80–150 µm long), marine or freshwater, loricate suctorian that varies from oval to triangular in outline, laterally flattened. Apical aperture slit-like or dumb-bell shape through which the two fascicles of capitate tentacles project. Cytoplasm usually confined within lorica but sometimes the lorica is reduced to small cup-like structure (Fig. 32n). Stalk long, usually several times the length of the lorica. Lorica sometimes striated transversely. Stalk always joins the lorica via a bulbous collar region forming a flexible joint. Reproduction by internal circuminvaginative budding (Kormos and Kormos, 1958). Sometimes several oval buds produced with eleven oblique ciliary rows each. Attached to the alga *Ulva.* Macronucleus ovoid, single apical contractile vacuole.

Note. Originally described by Keppen (1888), Collin (1912) stated it to be an easily identifiable species and included *Acineta compressa* as one of its synonyms. He stated that Claparède and Lachmann (1859) had distinctly figured its subglobular collar at the junction of stalk and lorica. In fact their diagram clearly shows that the collar of *A. compressa* has parallel sides and is not like the ovoid collar of *A. papillifera.* Collin (1912) also stated that reproduction resulted in a single bud whereas in another place in the same monograph he includes a diagram of multiple buds in *A. papillifera* (see Fig. 321). Kahl (1934) was of the opinion that *A. papillifera* Collin was not the same as *A. papillifera* Keppen and erected *A. collini* to distinguish the two. Here the two descriptions are considered to be of the same species. Recently, Jankowski (1978) erected the genus *Acinetella,* with *Acineta collini* Kahl as the type species, because of its possession of a hollow stalk and an oval collar. Since the present author has already stated that the two descriptions are thought to be the same it follows that *Acinetella* is a synonym.

Acineta parva Swarczewsky, 1928

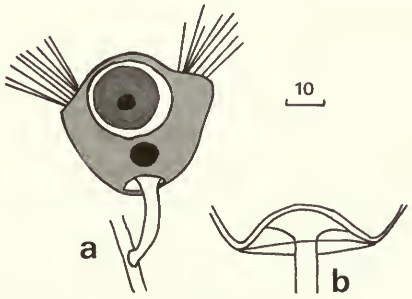

Fig. 33 *Acineta parva,* after Swarczewsky, 1928.

Description (Fig. 33). Small (30–40 µm long), freshwater, loricate suctorian species, laterally compressed, bell-shaped in outline. Apically, there is an oval aperture through which two fascicles of tentacles protrude. Actinophores present but reduced. Stalk short, 25–30 µm long, which joins the lorica via a spatula-shaped end embedded into a concavity in the posterior pole of the lorica. Reported from Lake Baikal as ectocommensal on the gammarid crustacean *Crypturopus tuberculatus*. Budding by monogemmic endogenous buds.

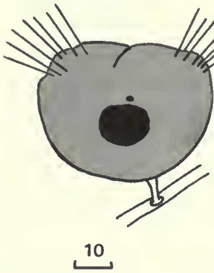

Fig. 34 *Acineta pugmaea*, after Swarczewsky, 1928.

Acineta pugmaea Swarczewsky, 1928

Description (Fig. 34). Small (30–40 µm long), freshwater, loricate suctorian with an oval outline, lateral compression weak, oval in cross-section. Anteriorly there is an oval aperture through which the low lobe-like actinophores and two fascicles of tentacles protrude. The stalk is shorter than the body length, 10 µm long, and attaches to the gammarid crustacea *Plesiogammarus gerstaeckeri* and *Crypturopus pachytus* in Lake Baikal. Large centrally located macronucleus present. Reproduction not described.

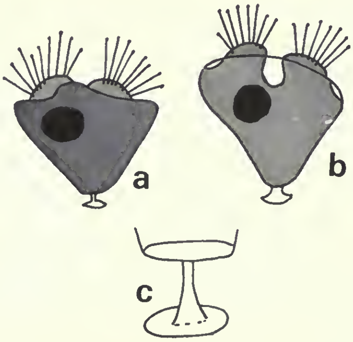

Fig. 35 *Acineta pulchra*, after Swarczewsky, 1928.

Acineta pulchra Swarczewsky, 1928

Description (Fig. 35). Small (30–35 µm long), freshwater, loricate species that is essentially triangular in outline, laterally compressed. Apically, the aperture is oval and sometimes there are flap-like extensions to the lorica so that the aperture rim is not always simply smooth as it is in most other species of the genus. Two actinophores moderately developed, each bearing a fascicle of tentacles. Stalk less than 5 µm long, joining the lorica via a wide but narrow strip-like collar (Fig. 35c). Reported from Lake Baikal attached to the gammarid crustacean *Odonthogammarus pulcherrimus* via a large circular basal plate.

Note. This species is not synonymous with *Acineta pulchra* Kahl, 1934 which as the junior synonym has been renamed *Acineta kahli* n. sp.

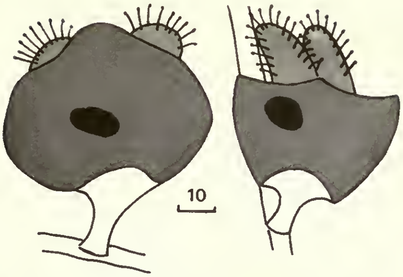

Fig. 36 *Acineta pumila*, after Swarczewsky, 1928.

Acineta pumila Swarczewsky, 1928

DESCRIPTION (Fig. 36). Small (45 µm long), freshwater, loricate suctorian that is oval to bell-shaped in outline, lightly compressed laterally. Aperture oval through which two well developed actinophores each bearing capitate tentacles protrude. Aperture rim not smooth, with flap-like lorica extensions and scalloped. Stalk short, 20 µm long, attached to the lorica via a spatulate-shaped end. Species reported from Lake Baikal attached to the gammarid crustacean *Gammarus kietlinskii*. Macronucleus spherical, reproduction not described.

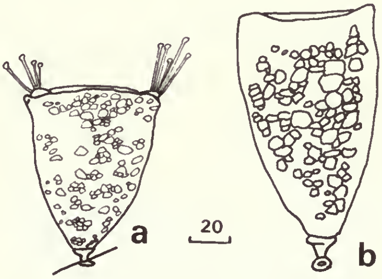

Fig. 37 *Acineta schulzi*, after Schulz, 1932 (called *A. tuberosa*).

Acineta schulzi (Schulz, 1932) Kahl, 1934

Acineta tuberosa Schulz, 1932

DESCRIPTION (Fig. 37). Medium to large (90–120 µm long) brackish, loricate suctorian with an inverted bell-shaped outline, laterally compressed. The lorica is covered in small particles of sand. Apically there is a dumb-bell shaped aperture through which the two fascicles of capitate tentacles emerge. Actinophores present. Stalk short, 10–15 µm long, joining the lorica via a cup-like end. Attached to copepods including *Tachidius brevicornis* (Precht, 1935). Nuclear and reproductive features not described.

NOTE. Originally described as a variety of *Acineta tuberosa* but was erected a species by Kahl (1934).

Acineta simplex Maskell, 1886

Acineta nieuportensis Sand, 1899

DESCRIPTION (Fig. 38). Small (35–50 µm long), fresh to brackish-water, loricate species that is goblet-shaped in outline, laterally compressed. There is an oval apical aperture through which two fascicles of capitate tentacles protrude. Actinophores reduced. Stalk medium, 35 µm long, attached to algae and inanimate objects in fresh and estuarine waters. There is a centrally located macronucleus and an off-centre contractile vacuole. Reproduction not described.

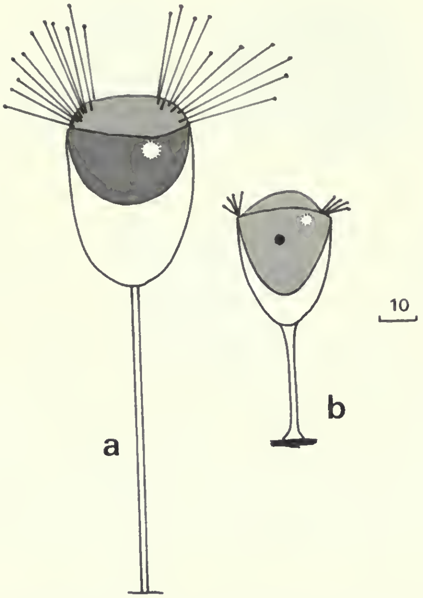

Fig. 38 *Acineta simplex,* (a) after Maskell, 1886; (b) after Sand, 1899.

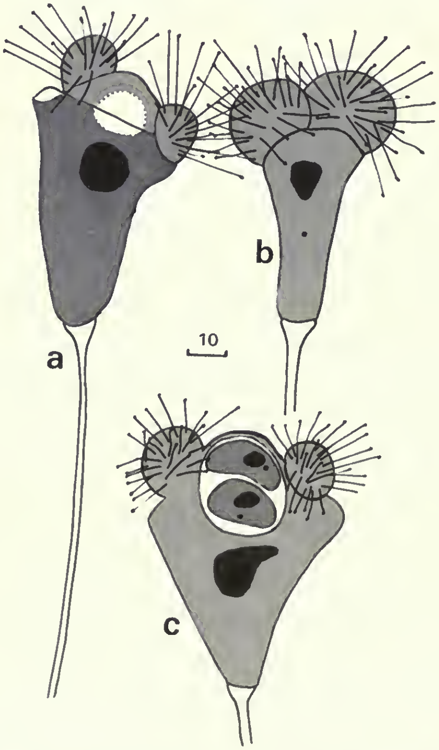

Fig. 39 *Acineta sphaerifera,* after Swarczewsky, 1928.

Acineta sphaerifera Swarczewsky, 1928

Tokophrya radiata Gajewskaja, 1933 *pro parte* (Fig. 138 only)

Description (Fig. 39). Medium (65–70 µm long), freshwater, loricate species with an elongated bell-shaped outline, weakly compressed laterally. Apically there is an oval aperture through which the two well developed spherical actinophores protrude. Each actinophore bears a fascile of capitate tentacles. Stalk at least 100 µm long, joining the lorica via a cup-like end. Reported from Lake Baikal attached to the gammarid crustacean *Ceratogammarus cornutus*. There is a centrally located macronucleus and an apical contractile vacuole. Reproduction by multiple endogenous bud formation.

Note. Gajewskaja (1933) described a variant of *Tokophrya radians* in Lake Baikal which has exactly the same appearance as *A. sphaerifera* and is treated here as a synonym, however this only refers to the variant illustrated in Fig. 138 of that work and not to *Tokophrya radians* in general.

Acineta sulcata Dons, 1928

Acineta benesaepta Schulz, 1933
Donsia sulcata (Dons, 1928) Jankowski, 1967
Plicophrya sulcata (Dons, 1928) Jankowski, 1975

Description (Fig. 40). Small (35–55 µm long), marine, loricate species with a corrugated almost rectangular outline, laterally compressed. The lorica is heavily striated or ridged transversely. There is a dumb-bell shaped apical aperture through which the two actinophores, each bearing a

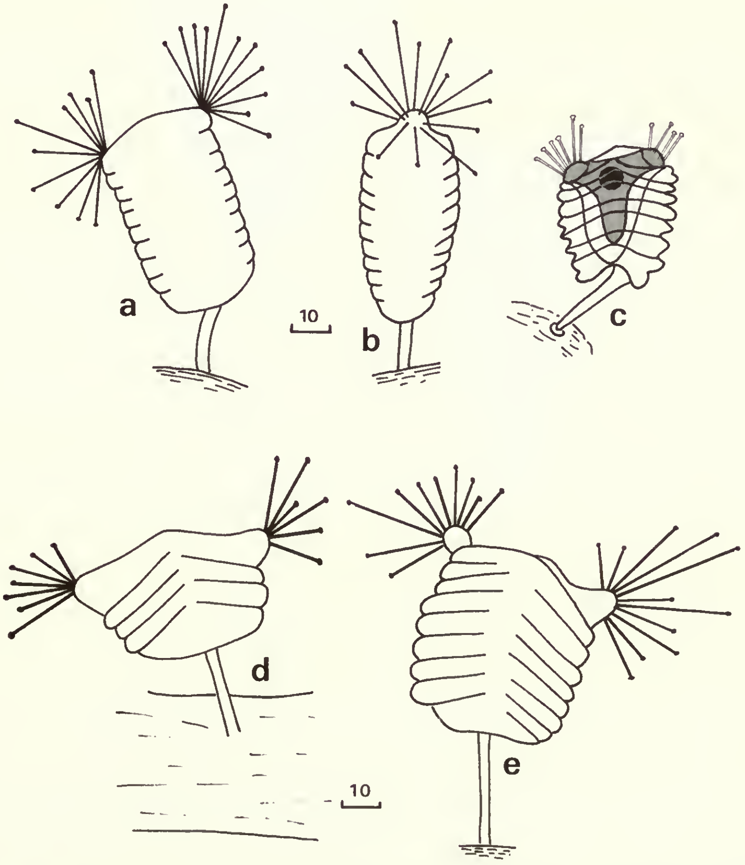

Fig. 40 *Acineta sulcata*: (a, b, d, e) after Dons, 1928; (c) after Schulz, 1933 (called *A. benesaepta*).

fascicle of captate tentacles, protrude. Stalk short, 20 µm long, with parallel sides attached to crustacea including the halacarid mite *Copidognathus fabriciusi,* and the ostracods *Hemicythere villosa* and *Cythereis tuberculata.* Macronucleus spherical, reproduction by monogemmic endogenous bud formation.

NOTE. *Acineta benesaepta* was transferred into *A. sulcata* by Kahl (1934). Jankowski (1967) was of the opinion that the presence of heavy transverse ridges on the lorica was sufficient to erect the new genus *Donsia* unfortunately the name was preoccupied by a mollusc. Jankowski (1975) therefore erected another generic name *Plicophrya* with *P. sulcata* as the type for the genus. The presence of heavy ridges on the lorica is not considered here to be sufficient to erect a new genus particularly since the type species for the genus *Acineta* is often heavily ridged.

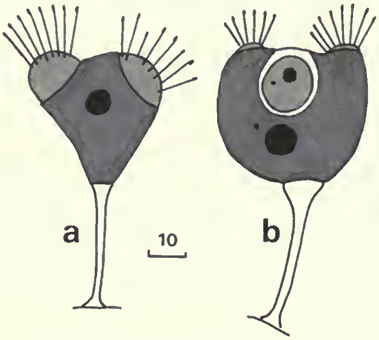

Fig. 41 *Acineta swarczewskia,* after Swarczewsky, 1928 (called *A. pusilla*).

Acineta swarczewskia (Swarczewsky, 1928) nom. nov.

Acineta pusilla Swarczewsky, 1928 (preoccupied by *Acineta pusilla* Maupas, 1881)

DESCRIPTION (Fig. 41). Small (35 µm long), freshwater, loricate species with an overall oval outline, compressed laterally. Apical aperture dumb-bell shaped with edges of lorica sometimes deeply cut away so that the actinophores emerge laterally as well as apically. In other specimens the lorica is not cut away and the two actinophores, each bearing a fascicle of capitate tentacles, slightly protrude anteriorly. Stalk medium, 40 µm long, joining the lorica via a cup-shaped end. Reported from Lake Baikal attached to the gammarid crustacea *Axelboeckia carpenteri, Ommatogammarus albinus* and *Odonthogammarus pulcherrimus.* Reproduction by monogemmic endogenous bud formation. Spherical macronucleus centrally located.

NOTE. This species was originally described under the name *A. pusilla,* a name preoccupied by another taxon *A. pusilla* Maupas, 1881. The latter has been transferred to the genus *Conchacineta* in this revision.

Acineta truncata Collin, 1909

Lecanophrya truncata Kahl, 1934

DESCRIPTION (Fig. 42). Small (40–50 µm long), marine or freshwater, loricate species with an inverted-bell outline, laterally compressed. The apical aperture is oval to dumb-bell shape. Actinophores reduced. Two fascicles of capitate tentacles on apical face of cytoplasm sometimes positioned so closely together that they almost merge into a single spreading group. Stalk short to medium 15–30 µm long, and sometimes wide, 10–15 µm, joining lorica either via a cup-like end or the sides may be parallel. Stalk always longitudinally striated. Attached to the harpacticoid copepod *Ameira.* Macronucleus spherical, centrally located. Contractile vacuole apical. Reproduction by internal budding (Gajewskaja, 1933).

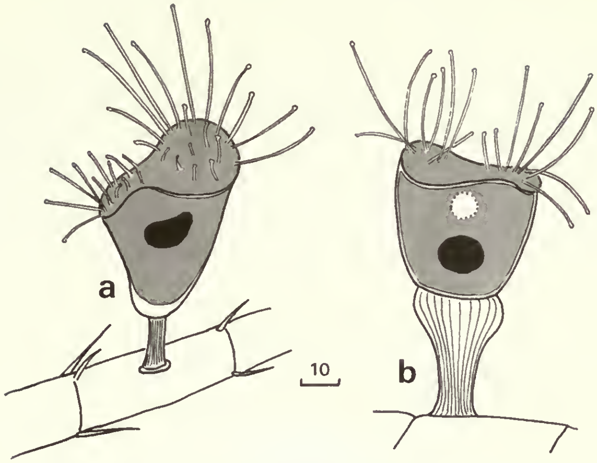

Fig. 42 *Acineta truncata*: (a) after Collin, 1912; (b) after Gajewskaja, 1933.

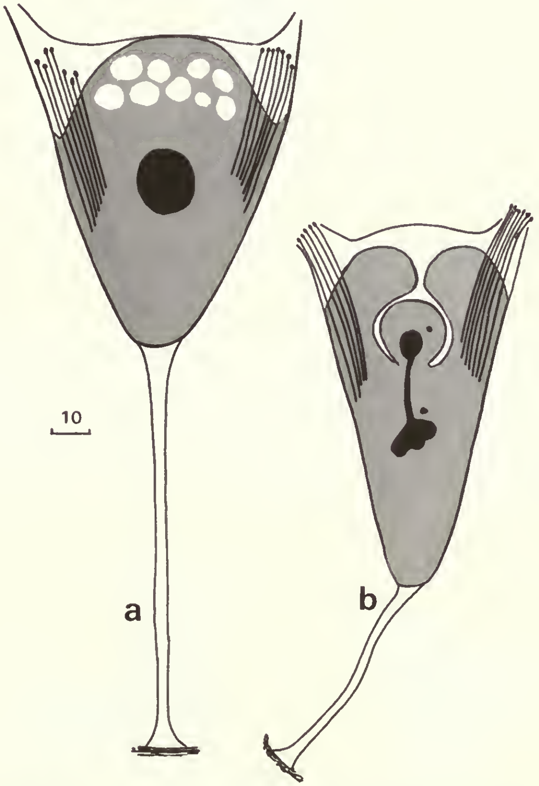

Fig. 43 *Acineta tubulifera*, after Swarczewsky, 1928.

NOTE. This species was originally described as a marine suctorian attached to harpacticoid copepods but later it was also reported from Lake Baikal (Gajewskaja, 1933). Kahl (1934) incorrectly transferred it into the genus *Lecanophrya* which only contains species that reproduce by exogenous budding.

Acineta tubulifera (Swarczewsky, 1928) n. comb.

Thecacineta tubulifera Swarczewsky, 1928

Description (Fig. 43). Medium to large (80–95 µm long), freshwater, loricate suctorian with a conical outline, laterally compressed. Structure of aperture distinctive, the apical end of the lorica is sealed leaving only two tube-like apertures through which the two fascicles of capitate tentacles protrude. Actinophores reduced. Stalk medium to long, 55–105 µm, joining the lorica via an expanded end. Reported from Lake Baikal attached to the gammarid crustacea *Axelboeckia carpenteri*, *Echinogammarus fuscus* and *Acanthogammarus godlewskii*. Centrally located spherical macronucleus. There are several apical contractile vacuoles. Reproduction by endogenous buds.

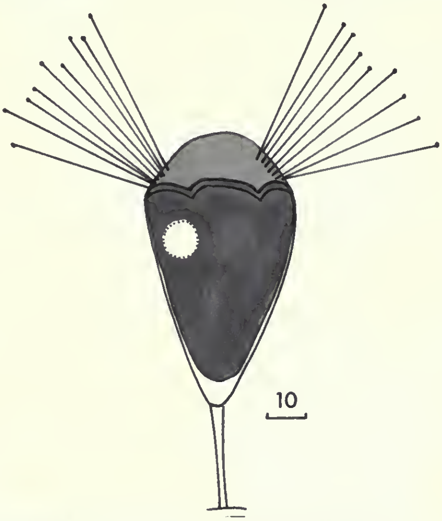

Fig. 44 *Acineta tulipa*, after Maskell, 1887.

Acineta tulipa Maskell, 1887

Description (Fig. 44). Medium (70 µm long), loricate, freshwater species whose outline resembles that of a tulip. The distinctive edge of the lorica aperture is scalloped to form five thickened lobes. Stalk short, 30 µm long. Actinophores reduced but the cytoplasm extends beyond the lorica aperture to form a dome. Two fascicles of capitate tentacles present. Contractile vacuole displaced to one side. Reported from New Zealand.

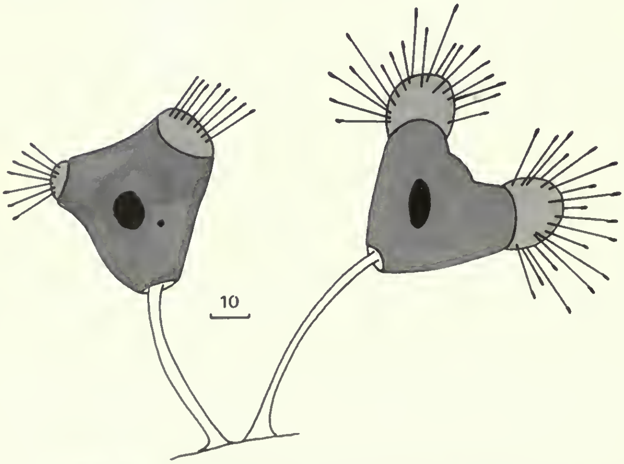

Fig. 45 *Acineta vulgata*, after Swarczewsky, 1928.

Acineta vulgata Swarczewsky, 1928

DESCRIPTION (Fig. 45). Small (40–50 µm long), freshwater, loricate species whose outline varies from triangular to Y-shape when the actinophores are particularly well developed. Flattened laterally. Actinophores lobe-like variable in size. Two fascicles of capitate tentacles present. Both actinophores and tentacles project through the oval apical lorica aperture. Stalk medium to long, 45–65 µm, joining the lorica via a conical collar embedded into a cavity in the terminal region of the lorica. Reported from Lake Baikal attached to the gammarid crustacea *Axelboeckia carpenteri, Odonthogammarus pulcherrimus, O. calcaratus, Acanthogammarus parasiticus, Parapallasea borowskii* and *Brandtia lata*. Spherical macronucleus centrally located.

Genus *ACINETIDES* Swarczewsky, 1928

Acineta Ehrenberg, 1833 *pro parte*
Periacineta Collin, 1909 *pro parte*

The genus *Acinetides* was erected by Swarczewsky (1928) as a single species genus for a suctorian found in Lake Baikal which possessed all the attributes of the genus *Acineta* except that it had a stylotheca rather than a real stalk. The genus *Periacineta* was originally set up by Collin (1909) for the suctorian *Hallezia buckei* (Kent) Sand, 1899–1901, however this, the type species, was transferred to the genus *Discophrya* Lachmann, 1859 by Matthes (1954). According to the International Code of Zoological Nomenclature this meant that the genus *Periacineta* became a junior synonym of *Discophrya* so that any species remaining in *Periacineta* would either need to be transferred to another appropriate genus or would need a new generic name. In the case in question, all nominal species that remained in *Periacineta* after the transfer of *Periacineta buckei* (Kent) Collin to *Discophrya* could be assigned to other genera. Some were transferred to other genera by Matthes (1954) and here some have been assigned to *Acinetides* for the first time.

Diagnosis of *Acinetides*

Marine or freshwater suctorians whose outline varies from triangular to bell-shape and which are strongly laterally compressed. Stylotheca, a lorica whose posterior region is elongated to form a stalk-like appendage present. Two actinophores present, each bearing a fascicle of capitate tentacles which protrude through the apical slit-like aperture. Tentacles absent in one species. Reproduction by monogemmic endogenous budding producing ovoid buds whose ciliary pattern remains undescribed. Suctorian attached to a variety of substrata including algae, crustacea and inanimate objects.

Key to the species of *Acinetides*

1	Marine	2
	Freshwater	3
2	Actinophores distinct, cell wider than long	***A. symbiotica***
	Actinophores indistinct, cell longer than wide	***A. gruberi***
3	Cell contents extend into stalk region	4
	Cell contents do not extend into stalk region	6
4	Bell-shaped, cell contents extend down to base of stalk	5
	Elongated-triangular shape, cell contents extend part way down stalk region	***A. varians***
5	Anterior contractile vacuole, body length twice body width	***A. lacustris***
	Posterior contractile vacuole, body width almost equal to body length	***A. urceolata***
6	With tentacles.	7
	Without tentacles	***A. labiata***
7	Body triangular, width almost equal to body length	***A. triangularis***
	Body bell-shape, body length twice width	***A. lacustris***

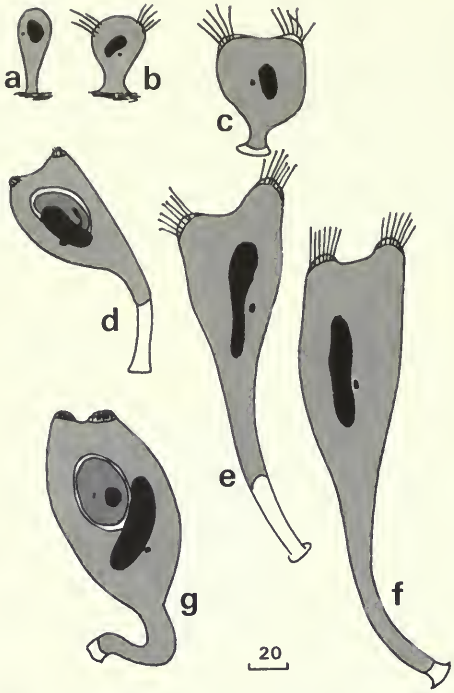

Fig. 46 *Acinetides varians,* after Swarczewsky, 1928.

Species descriptions

Acinetides varians Swarczewsky, 1928

Description (Fig. 46). This type species is a freshwater suctorian that has an elongated triangular outline and is laterally compressed. Fully grown specimens are large (240 µm long) but immature ones vary from about 40 µm long upwards. Variation in outline at different growth stages are illustrated in Fig. 43a–f. Two actinophores each bearing a fascicle of capitate tentacles protrude through an apical slit-like aperture. The lorica extends posteriorly to form a stalk-like stylotheca which is partially filled with cytoplasm. The species has only been described from Lake Baikal (Swarczewsky, 1928) where it was found attached to the amphipod *Poeckilogammarus pictus*. There is a centrally located elongated ovoid macronucleus. Reproduction by monogemmic endogenous budding.

Acinetides gruberi (Gruber, 1884) n. sp.

Acineta sp. Gruber, 1884
Acineta tuberosa Collin, 1912 *pro parte*

Description (Fig. 47). Large (200 µm long), loricate, marine suctorian whose length is approximately twice its width, laterally compressed. Lorica extends posteriorly to form a stalk-like stylotheca. Anteriorly the lorica has a slit-like aperture through which two fascicles of capitate tentacles protrude. Reproduction by monogemmic endogenous budding.

Note. This species was transferred by Collin (1912) to *Acineta tuberosa,* however the presence of a stylotheca does not allow its inclusion in that genus.

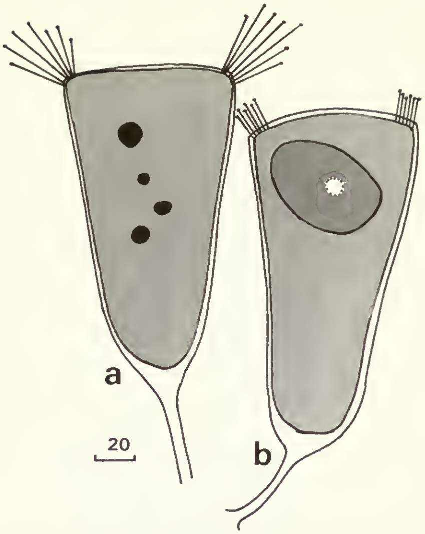

Fig. 47 *Acinetides gruberi,* after Gruber, 1884 (called *Acineta* sp.).

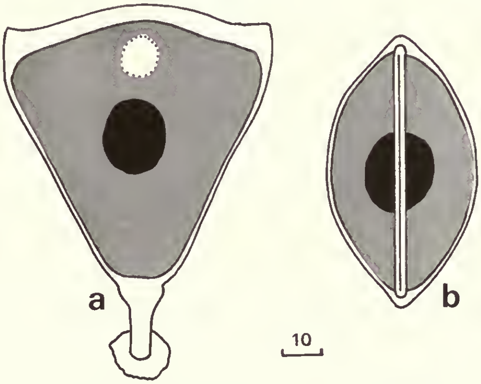

Fig. 48 *Acinetides labiata,* after Rieder, 1936 (called *Acineta labiata*).

Acinetides labiata (Rieder, 1936) n. comb.

Acineta labiata Rieder, 1936

Description (Fig. 48). Freshwater, medium (80 µm long), loricate suctorian that is laterally compressed and triangular in outline. Anteriorly the lorica has a slit-like aperture but tentacles are apparently absent and actinophores are reduced. Posteriorly the lorica forms a short, 15 µm long, thecostyle with a prominent basal disc-like plate. Stylotheca does not contain cytoplasm. Contractile vacuole apically located, spherical macronucleus in centre of body.

Acinetides lacustris (Stokes, 1886) n. comb.

Acineta lacustris Stokes, 1886
Periacineta lacustris Penard, 1920

Description (Fig. 49). Freshwater, large (100–180 µm long), loricate suctorian, laterally compressed. Anteriorly the lorica has a slit-like aperture through which the two actinophores

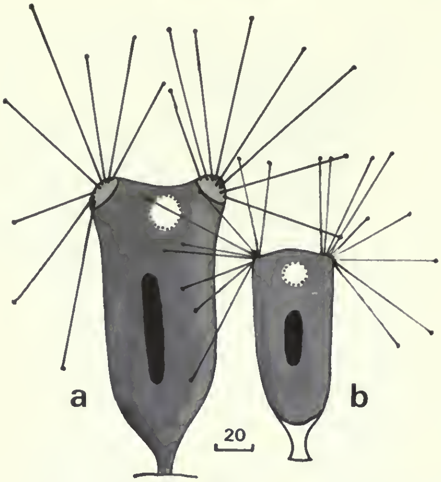

Fig. 49 *Acinetides lacustris*: (a) after Stokes, 1886 (called *Acineta lacustris*); (b) after Penard, 1920 (called *Periacineta lacustris*).

each bearing a fascicle of capitate tentacles protrude. Posteriorly the lorica is extended to form a short, 20 μm, stylotheca which may or may not be filled with cytoplasm. Found in ponds attached to *Anacharis* sp. Single centrally located elongate macronucleus and an anterior contractile vacuole.

Acinetides symbiotica (Daday, 1907) n. comb.

Acineta symbiotica Daday, 1907
Acineta calix Daday, 1907
Acineta calyx Daday, 1910

Description (Fig. 50). Small to medium (35–55 μm long), loricate suctorian, approximately triangular in outline and laterally compressed. Anteriorly the lorica has a slit-like aperture through which the two actinophores each bearing ,a fascicle of capitate tentacles protrude. Posteriorly the lorica is extended to form a short, 15 μm, stylotheca which is not filled with cytoplasm. Found attached to either the colonial green alga *Botryococcus (Botryomonas) natans* Schmidt or to the post-mysis larva of the crustacean *Caridina wyckii*. Macronucleus located central to posterior. Reproduction not described.

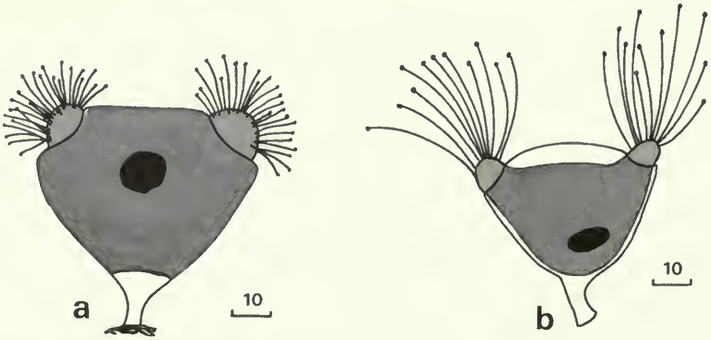

Fig. 50 *Acinetides symbiotica*: (a) after Daday, 1907 (called *Acineta calix*): (b) after Daday, 1907.

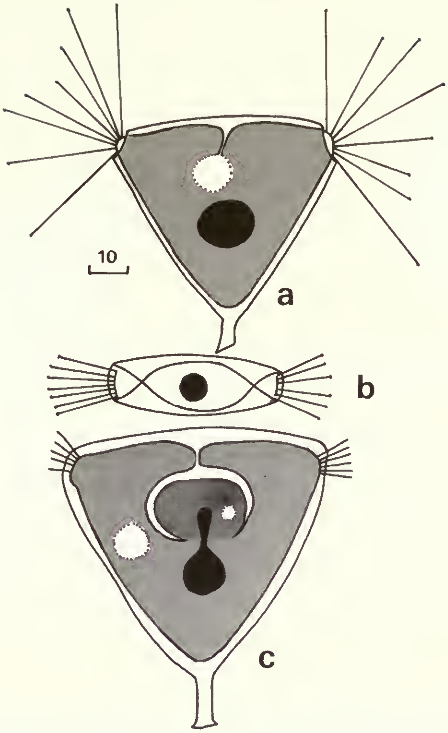

Fig. 51 *Acinetides triangularis,* after Penard, 1920 (called *Periacineta triangularis*).

Acinetides triangularis (Penard, 1920) n. comb

Periacineta triangularis Penard, 1920
Acineta triangularis Matthes, 1954

Description (Fig. 51). Freshwater, medium (50 µm long), loricate suctorian that has an equilateral triangular outline, strongly compressed laterally. The lorica has a dumb-bell slit-like aperture through which two fascicles of capitate tentacles protrude. Posteriorly the lorica extends into a short, 10 µm, stylotheca. There is a centrally placed spherical macronucleus and a laterally located contractile vacuole. Reproduction by monogemmic endogenous budding.

Acinetides urceolata (Stokes, 1885) n. comb.

Acineta urceolata Stokes, 1885
Periacineta urceolata Collin, 1909

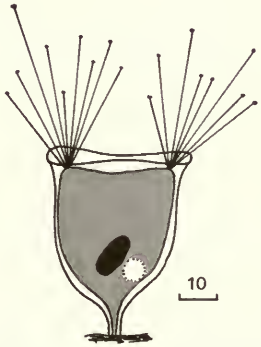

Fig. 52 *Acinetides urceolata,* after Stokes, 1885*a* (called *Acineta urceolata*).

Description (Fig. 52). Freshwater, small to medium (40 µm long), loricate suctorian with a bell-shaped outline, laterally compressed. There is a dumb-bell slit-like aperture and two fascicles of capitate tentacles. The stylotheca is short, 10 µm, and contains a strand of cytoplasm, attached to aquatic plants. Both the ovoid macronucleus and the contractile vacuole in a posterior location.

Note. Originally described by Stokes (1885*a*).

Genus *CONCHACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*
Nematacineta Jankowski, 1978
Soracineta Jankowski, 1978

The genus *Conchacineta* was erected by Jankowski (1978) on the basis of the following brief note, '*Conchacineta* (*Ac. constricta* Collin; with rows of tentacles)', where the type species and main distinguishing character are given in parentheses. The tentacles of certain other species of suctoria are also arranged in rows rather than in bundles, but in some of these cases it would be highly inappropriate to include them in a genus along with *Acineta constricta* Collin. This suggests that the original description was not sufficiently well defined, furthermore another genus, *Nematacineta,* erected in the same publication (Jankowski, 1978) was also said to have an arcuate row of tentacles. In spite of this, the generic name has been retained for the sake of taxonomic stability and the diagnosis expanded to include both genera.

Diagnosis of *Conchacineta*

Marine suctorians whose outline shape varies from oval to pyriform; laterally flattened. Actinophores absent. Capitate tentacles arranged as a single row in two fascicles. The latter may be difficult to distinguish in some species if set close together. Tentacles protrude through an apical dumb-bell shaped slit in the lorica. A stalk attaches the suctorian to a variety of substrates including hydrozoa, crustacea, nematodes, polychaete worms and inanimate objects. In one species the stalk has been reported to be missing occasionally as sometimes happens in the genus *Podophrya*. Macronucleus spherical. Endogenous monogemmic budding has been reported in 2 species. Ciliation of the oval larva arranged in 10 oblique to longitudinal rows.

Key to the species of *Conchacineta*

1	Body borne upon stalk		2
	Stalk absent, attached by tentacles	*C. complatana*	
2	Lorica with definite waist-like indentation	*C. constricta*	
	Lorica without waist		3
3	Width of body greater than length		4
	Length of body greater than width		6
4	Lorica narrows towards stalk		5
	Lorica very wide near stalk	*C. complatana*	
5	Stalk wide (about 8 µm). Epizoic on crustacea	*C. amphiasci*	
	Stalk narrow (about 2 µm). Epizoic on bryozoa and hydrozoa	*C. pusilla*	
6	Stalk striated transversely, apex of body rounded Epizoic on nematodes	*C. rotunda*	
	Stalk smooth, apex of body truncate	*C. ovata*	

Species descriptions

Conchacineta constricta Jankowski, 1978

Acineta constricta Collin, 1909

Description (Fig. 53). This the type species, is almost circular in outline, approximately 70 µm in diameter, with a distinctive central waist-like indentation on each lateral edge. The lorica is

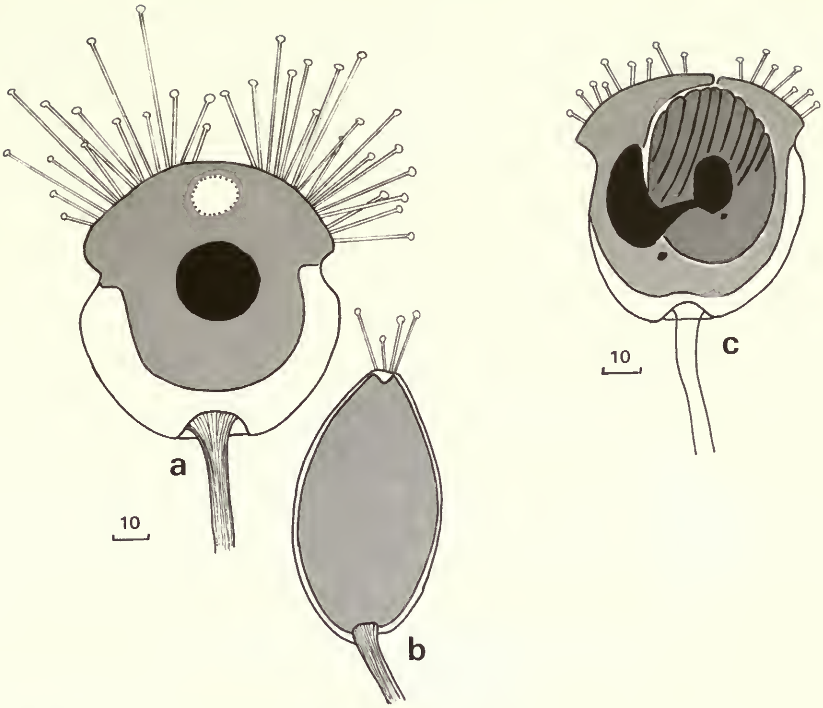

Fig. 53 *Conchacineta constricta,* after Collin, 1912 (called *Acineta constricta*).

strongly compressed laterally and open anteriorly via a slit-like aperture through which the 2 fascicles of capitate tentacles protrude. The tentacles are arranged as a row in each fascicle. The lorica is mounted on a longitudinally striated stalk attached to crustacea such as *Pagurus cuanensis* Thompson. There is a single centrally located macronucleus and an anterior contractile vacuole. Endogenous, monogemmic budding results in a relatively large, 50 × 35 µm, ovoid bud bearing 10 obliquely orientated rows of cilia.

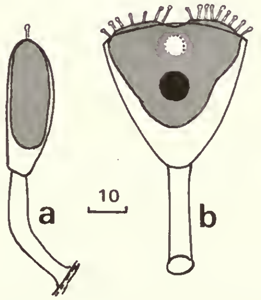

Fig. 54 *Conchacineta amphiasci,* after Precht, 1935 (called *Acineta amphiasci*).

Conchacineta amphiasci (Precht, 1935) n. comb.

Acineta amphiasci Precht, 1935

Description (Fig. 54). Marine suctorian that is pyriform to triangular in outline, strongly compressed laterally and is about 27–50 µm long. The lorica has an anterior slit-like aperture through which the short capitate tentacles protrude. The tentacles are arranged as a single row in each of the 2 fascicles. The stalk is relatively wide, 8 µm, and serves to attach the lorica to the copepod *Amphiascus typhlops*. There is a central macronucleus and an anterior contractile vacuole. Budding has not been described.

Conchacineta complatana (Gruber, 1884) n. comb.

Acineta complatana Gruber, 1884
Acineta complanata Collin, 1912
Soracineta complanata Jankowski, 1978

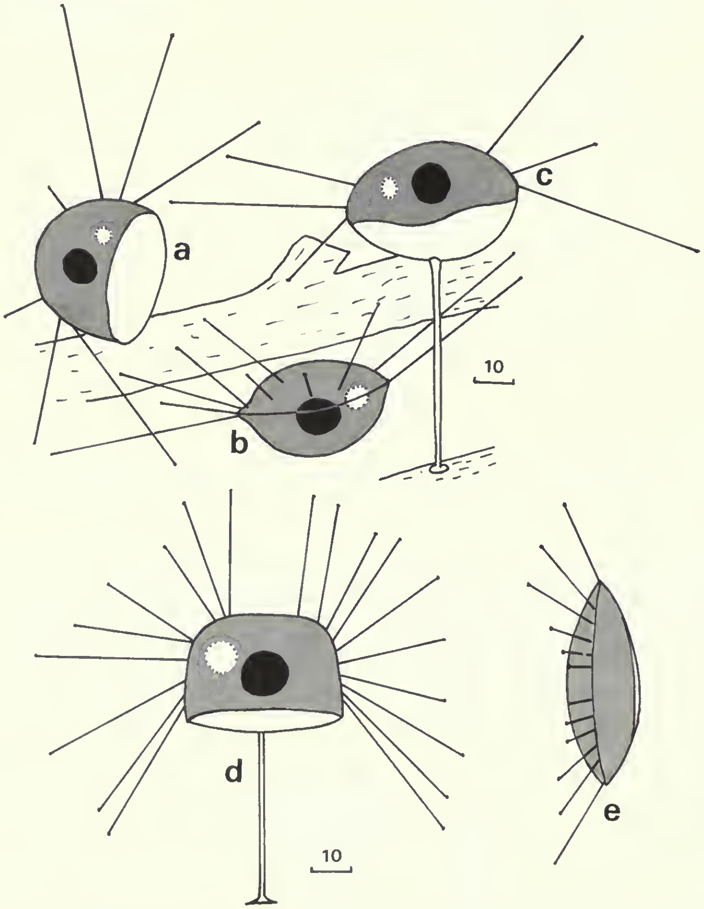

Fig. 55 *Conchacineta complatana*: (a–c) after Collin, 1912 (called *Acineta complanata*); (d, e) after Gruber, 1884 (called *Acineta complatana*).

Description (Fig. 55). Marine suctorian that is strongly oval in outline, laterally flattened and is wider than deep (40 × 30 µm). The lorica is open anterio-laterally via a slit-like aperture through which two fascicles of long, 50 µm, capitate tentacles protrude. The tentacles are arranged as a single row in each of the fascicles. The body is normally mounted on a long, 60 µm, stalk but occasionally may become detached when the suctorian attaches itself to the substratum or to its prey using its tentacles. The stalk is usually attached to hydrozoa, such as *Halecium beanii* Johnston, or to bryozoa. There is a single centrally placed macronucleus and a laterally located contractile vacuole. The mode of budding has not been described.

Note. The specific name was originally quite clearly spelt as *'complatana'* by Gruber but Collin (1912) and subsequent authors have all mis-spelt it as *'complanata'*. Jankowski (1978) set up the

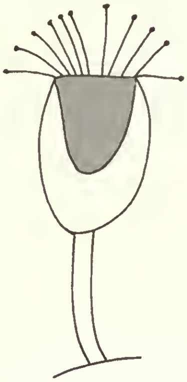

Fig. 56 *Conchacineta ovata,* after Pritchard, 1852.

genus *Soracineta* Jankowski, 1978 for this species using the following brief phrase '*Soracineta* (*Ac. complanata* Gruber; with semilorica)', however there are several other genera of suctoria containing partially loricate species and this is not considered sufficient grounds on which to erect a new genus.

Conchacineta ovata (Pritchard, 1852) n. comb.

Alderia ovata Pritchard, 1852
Podophrya ovata Wright, 1858

Description (Fig. 56). Marine, loricate oval suctorian whose anterior end is bluntly truncate. The capitate tentacles emerge from the lorica in a single row at the apex of the cell. Stalk approximately same length as lorica attached to hydroid colonies such as *Sertularia*. Size unrecorded. Budding and internal structures not described.

Note. An incompletely described species that has been placed in the genus *Conchacineta* because of the arrangement of the tentacles. Originally described without a name by Alder (1851).

Conchacineta pusilla (Maupas, 1881) n. comb.

Acineta pusilla Maupas, 1881 (not *Acineta pusilla* Swarczewsky, 1928)
Acineta emaciata Maupas, 1881
Acineta parva Sand, 1899 (*not Acineta parva* Swarczewsky, 1928)
Paracineta parva Collin, 1912
Paracineta parva Wailes, 1943

Description (Fig. 57). Marine, loricate, oval to lozenge shaped suctorian whose cytoplasm rarely fills the lorica. There is a dumb-bell shaped aperture at the apex of the cell through which the short, 10 µm, tentacles protrude. Tentacles arranged in 2 fascicles as a single row in each. Stalk tends to be short but varies between 10–20 µm in length. Size also variable but this probably reflects different stages in the cell's growth. Small. 10 µm wide, oval forms tend to be wider than deep. Older forms are larger, 50 × 60 µm. Found attached to a variety of substrates including algae, bryozoa and the tubes of the polychaete worm *Phyllochaetopterus prolifica*. Macronucleus ovoid to spheroid, contractile vacuole located laterally. Monogemmic endogenous bud formation described but details of the buds were not recorded (Maupas, 1881).

Note. Although Maupas (1881) described *Acineta pusilla* and *Acineta emaciata* in the same publication, the description of the former species appeared a few pages before that of the latter, thus *Acineta pusilla* takes priority. The species *Acineta pusilla* Maupas, 1881 should not be confused with *Acineta pusilla* Swarczewsky, 1928 see p. 106.

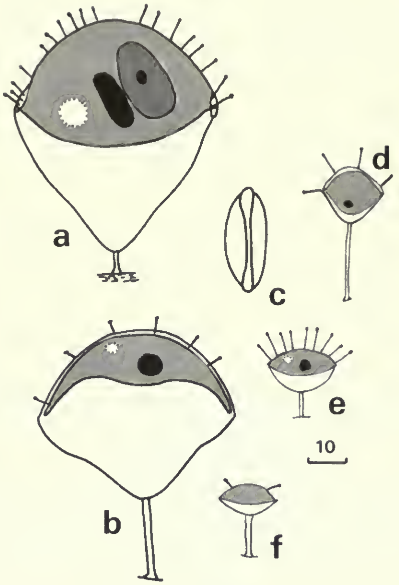

Fig. 57 *Conchacineta pusilla*: (a–c, f) after Maupas, 1881 (called *Acineta emaciata*); after Maupas, 1881; (e) after Wailes, 1943 (called *Paracineta parva*).

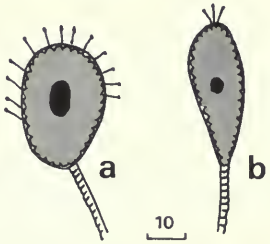

Fig. 58 *Conchacineta rotunda*, after Allgen, 1952; (a) called *Acineta rotunda*; (b) called *Acineta ovoidea*.

Conchacineta rotunda Allgén, 1952

Acineta rotunda Allgén, 1952
Acineta ovoidea Allgén, 1952
Nematacineta rotunda Jankowski, 1978

Description (Fig. 58). Oval, laterally compressed marine suctorian found attached to the nematode worm *Desmadora*. Capitate tentacles arranged in a single row around the anterio–lateral edges of the lorica. Stalk shorter than body length, striated transversely. Macronucleus centrally located. Reproduction not described.

Note. Allgén (1952) described 2 species of *Acineta* occurring together on the nematode *Desmadora*. The second of the 2 species, *Acineta ovoidea*, has been interpreted here to be *Acineta rotunda* viewed from the edge and thus illustrating the lateral compression that is common in these genera of suctorians. The genus *Nematacineta* Jankowski, 1978 was erected with the phrase '*Nematacineta* (*Ac. rotunda* Allgen; with an arcuate row of tentacles)'. This brief description alone is insufficient to erect a new genus since it falls within the limits of the previously described *Conchacineta* Jankowski, 1978.

Genus *CROSSACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*

The genus *Crossacineta* was erected by Jankowski (1978) on the basis of the following brief diagnosis '*Crossacineta* (*Ac. ornata* Sand; lorica with annular ribs)' where the type species and main diagnostic character are given in parenthesis. The lorica of one other previously described species, *Acineta annulata* Wang and Nie, 1933 is also heavily ribbed and this has been included in the genus *Crossacineta* for the first time.

Diagnosis of *Crossacineta*

Marine or brackish water suctorians whose outline shape is approximately pyriform and oval in cross-section. The lorica is heavily ribbed transversely and there is an oval apical aperture through which the cell and its 2 fascicles of capitate tentacles protrude. Actinophores absent. The stalk is about 1/3 length of the lorica and the cell is attached to marine algae and hydrozoa. Macronucleus spherical. Budding not described.

Key to the species of *Crossacineta*

1	Ribs sharply project beyond lorica edge. Ribs separated by unribbed parts of the lorica	***C. ornata***
	Rounded ribs do not project beyond lorica edge. Lorica totally ribbed, without non-ribbed parts	***C. annulata***

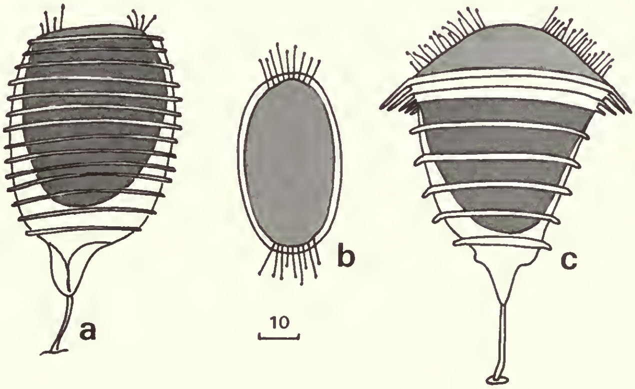

Fig. 59 *Crossacineta ornata,* after Sand, 1899 (called *Acineta ornata*).

Species descriptions

Crossacineta ornata (Sand, 1899) Jankowski, 1978

Acineta ornata Sand, 1899

Description (Fig. 59). This the type species is found in brackish waters. It is medium sized (70 µm long) and may be immediately distinguished by the heavy transverse ribs on its lorica which project out laterally. The ribs are interspersed with smooth areas of the lorica which is oval in cross-section. The animal is mounted on a short, 20 µm long, thin stalk that is attached to algae via a circular basal plate. Anteriorly there is an oval aperture through which the cell and its 2 fascicles of capitate tentacles protrude. Actinophores absent. Budding and buds remain undescribed.

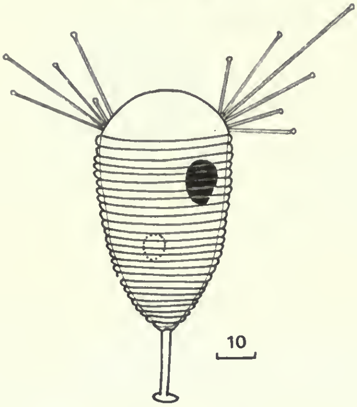

Fig. 60 *Crossacineta annulata* after Wang & Nie, 1933 (called *Acineta annulata*).

Crossacineta annulata (Wang and Nie, 1933) n. comb.

Acineta annulata Wang and Nie, 1933

Description (Fig. 60). Marine, medium (65 μm long) suctorian whose corrugated lorica is composed of many transverse rows of rounded ribs which increase in number as the animal grows. The body is oval in cross-section. The lorica is mounted on a short stalk, 20 μm long, and is attached to seaweeds or hydrozoa such as *Sertularia* sp. Anteriorly there is an oval aperture through which the cell and its 2 fascicles of capitate tentacles protrude. Actinophores absent. The spherical to oval macronucleus is in the anterior half of the body and the contractile vacuole in the posterior third. Budding and buds not described.

Genus *CRYPTACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*

The genus *Cryptacineta* was erected by Jankowski (1978) on the basis of the following brief remark '*Cryptacineta* (*Ac. operata* Swarc.; with mucous lorica)' where the type species, incorrectly spelt, and major distinguishing feature are given in parenthesis. Since *Acineta operta* Swarczewsky, 1928 is the only species of that genus possessing a mucoid lorica and since it also lacks actinophores then the genus erected by Jankowski (1978) has been accepted here but has been rather more fully defined below.

Diagnosis of *Cryptacineta*

Freshwater suctorian whose outline varies from oval to tulip-shape. The lorica is thick and mucoid in nature, totally enveloping the cell and stalk base. Anteriorly the two fascicles of tentacles project through an aperture of undefined shape. Actinophores absent. Posteriorly the stalk projects through the lorica. Attached to gammarid crustaceans. Budding type and buds remain undescribed. Macronucleus ovoid. Single species genus.

Description of species

Cryptacineta operta (Swarczewsky, 1928) Jankowski, 1978

Acineta operta Swarczewsky, 1928
Cryptacineta operata Jankowski, 1978

Description (Fig. 61). This the type species is found in Lake Baikal. It is a small–medium

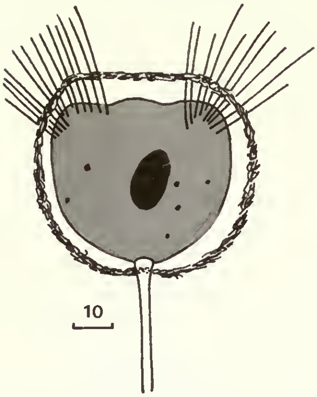

Fig. 61 *Cryptacineta operta,* after Swarczewsky, 1928 (called *Acineta operta*).

(50–60 µm long) suctorian whose thick mucoid lorica completely envelops the stalked tulip-shaped body. Anteriorly there are 2 fascicles of tentacles projecting through the lorica while posteriorly the stalk also penetrates the surrounding lorica. Reproduction and type of buds remain undescribed. Macronucleus ovoid. Attached to the two gammarid crustaceans *Carinogammarus seidlizi* and *C. wagneri.*

Genus ***KELLICOTTA*** n. gen.

Acineta Ehrenberg, 1833 *pro parte*

The species *Acineta cuspidata* Kellicott, 1885 differs markedly from other species in that genus in several respects. Firstly, it has long capitate tentacles which Kellicott (1885) described to have 'a writhing searching motion like that of the arms of the common *Hydra'*. Tentacles such as these are completely unlike any of those known in other members of the genus. Secondly, the body is oval in outline and there are no lobe-like actinophores which are usually seen in *Acineta.* Finally the body was described by Kellicott (1885) to be 'spheroidal or sub-cylindrical' without mention of lateral compression as found in *Acineta.* For these reasons this species cannot be fitted into the genus *Acineta* nor into any other previously described genus including *Podocyathus (Actinocyathus)* as tentatively suggested by Kellicott (1885). It has therefore been necessary to erect the new genus *Kellicotta* with *Kellicotta cuspidata* (Kellicott, 1885) n. comb. as the type species.

Diagnosis of *Kellicotta*

Freshwater suctorians, ovoid, not laterally compressed. Lorica cup-shaped borne on short rigid stalk, apical aperture oval to round in outline. Actinophores absent Tentacles long with writhing action, capitate arranged in two fascicles projecting out beyond aperture rim. Mode of reproduction unknown, buds not described. Attached to aquatic plants. Single species genus.

Key to species of *Kellicotta*

1 Lorica has two prominent cusps forming the aperture rim . . . . **K. cuspidata**

Species description

Kellicotta cuspidata (Kellicott, 1885) n. comb.

Acineta cuspidata Kellicott, 1885

Description (Fig. 62). Small (40 µm long), ovoid, freshwater suctorian housed in a cup-like lorica which has two distinctive cusps forming the rim of the aperture. Actinophores absent.

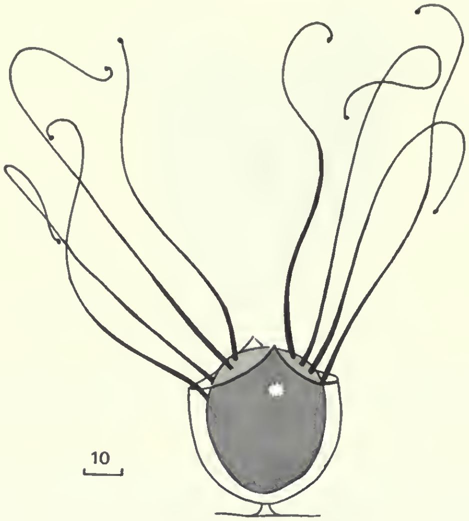

Fig. 62 *Kellicotta cuspidata*, after Kellicott, 1885 (called *Acineta cuspidata*).

Two fascicles of long, 2–3 times body length, capitate tentacles that are capable of a writhing, searching action. Lorica borne upon a short, less than 5 µm long, rudimentary stalk attached to freshwater algal filaments (*Oedogonium*). Single contractile vacuole located in the anterior body third. Reproduction undescribed.

Genus *PHYLLACINETA* Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*
Ternacineta Jankowski, 1978

The genus *Phyllacineta* was erected by Jankowski (1978) using the following brief note, '*Phyllacineta* (*Acineta jolyi* Maupas; with three actinophores)' where the data in parentheses refer to the type species and major distinguishing character respectively. While the description is brief it is nevertheless sufficient for the specialist to be able to understand and accept his proposal. The feature which distinguishes the two species in this genus from *Acineta* is their possession of three fascicles of tentacles borne upon short actinophores. Additionally, although not perfectly clear from the original descriptions, it would appear that there are three separate apertures in the lorica rather than a single elongated dumb-bell shaped slit as in *Acineta*. For these reasons the proposal of Jankowski (1978) is supported and a full emended diagnosis is given below.

Diagnosis of *Phyllacineta*

Marine or freshwater suctorians. Outline appearance of body varies from an oval to irregular diamond shape; laterally flattened. There are 3 low lobe-like actinophores present, 1 at the cell apex and 2 on either lateral body edge. Tentacles, either simply capitate or with expanded trumpet-like ends, grouped in 3 fascicles which protrude through the lorica via 3 separate apertures. Lorica attached by a stalk to crustacea, hydrozoa, bryozoa or algae. Macronucleus spherical. Asexual reproduction by simple endogenous monogemmic budding producing ovoid migratory larvae bearing 5 transversal rings of cilia.

Key to the species of *Phyllacineta*

1 Marine, with stalk as long as approximately diamond-shaped body. With single contractile vacuole, tentacles simply capitate . . . . ***P. jolyi***
Freshwater, stalk approximately a quarter of the length of the ovoid body. With 1–3 contractile vacuoles, tentacles with trumpet-ends . . . . ***P. tripharetrata***

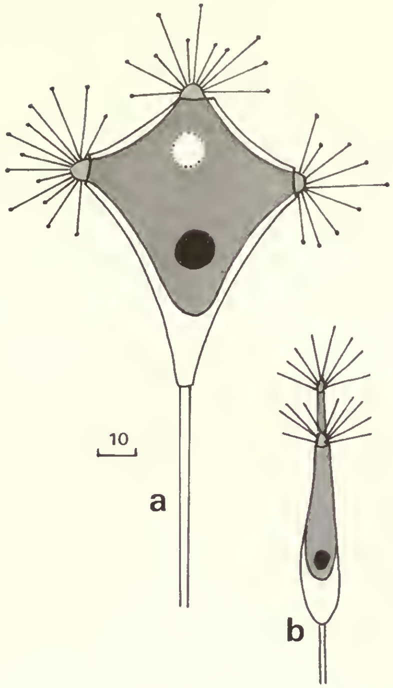

Fig. 63 *Phyllacineta jolyi*, after Maupas, 1881 (called *Acineta jolyi*).

Species descriptions

Phyllacineta jolyi (Maupas, 1881) Jankowski, 1978

Acineta jolyi Maupas, 1881

Description (Fig. 63). This, the type species, is approximately 80 µm long and is irregularly diamond-shaped in outline. The lorica is strongly compressed laterally and is pierced by three apertures through which the three short actinophores, bearing simple capitate tentacles, protrude. The lorica is mounted on a stalk that is at least the length of the lorica and attached distally to marine algae, hydrozoa or bryozoa. There is a single, anteriorly located, contractile vacuole and a posterior spherical macronucleus.

Phyllacineta tripharetrata (Entz, 1902) n. comb.

Acineta tripharetrata Entz senior, 1902
Ternacineta tripharetrata Jankowski, 1978

Description (Fig. 64). The low conical body, almost triangular in some specimens, narrows anteriorly and measures about 45 µm in length by 115 µm wide. The lorica although compressed is not so strongly flattened as in the type species, however, it is pierced by 3 apertures through which the 3 fascicles of tentacles protrude. The acinophores are not easy to distinguish but in some specimens there is a definite tendency for the body to form low lobes in the vicinity of the fascicles. The tentacles are reminiscent of those in *Choanophrya*, being rather 'baggy' in appearance with expanded trumpet-like tips. The lorica is mounted on a short stalk, 10 µm, attached to freshwater crustacea such as *Daphnia pulex* and *Cyclops phaleratus*. There are 1–3 contractile vacuoles located across the broad posterior end of the cell. The ovoid macronucleus is centrally located. Endogenous, monogemmic budding results in a large, 50 × 40 µm, ovoid bud bearing 5 transverse ciliary rings and sexual reproduction by conjugation has been described by Entz (1902).

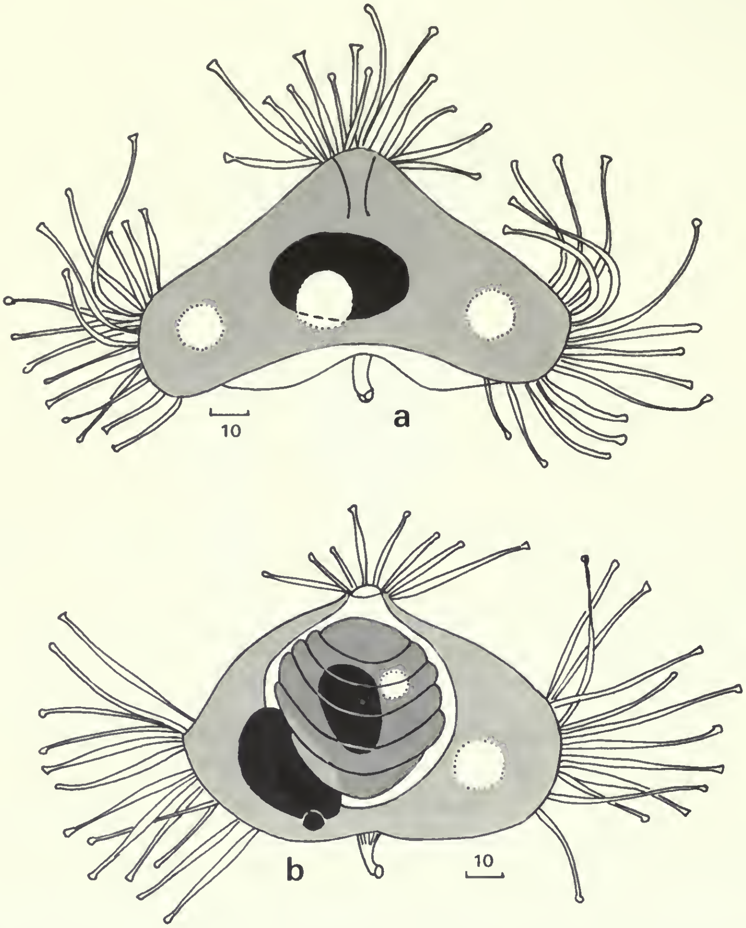

Fig. 64 *Phyllacineta tripharetrata,* after Entz, 1902 (called *Acineta tripharetrata*).

Note. The genus *Ternacineta* Jankowski, 1978 was erected on the basis of the following brief note '*Ternacineta* (*Ac. tripharetrata* Entz, with three bunches of tentacles)'. It is here considered to be unnecessary to erect a single species genus when it can quite easily be fitted into the genus *Phyllacineta* Jankowski, 1978 which also has 3 bunches of tentacles. However, actinophores are not easy to distinguish in this species and its tentacles are of a different structure to those of the type species. More observations on specimens are needed to confirm the true taxonomic position of this species.

Genus ***VERACINETA*** Jankowski, 1978

Acineta Ehrenberg, 1833 *pro parte*

The genus *Veracineta* was erected by Jankowski (1878) on the basis of the brief phrase, '*Veracineta* (*Ac. tisbei* Guilcher; with apical tentacles)' where the type species and main distinguishing feature are given in parenthesis. Since all described *Acineta* spp. have tentacles arranged more or less apically then this can hardly be precisely what Jankowski (1978) meant. Presumably he intended to indicate that the presence of a single fascicle of apical tentacles was the salient feature and it is this interpretation that has been used here. The tentacles of one other previously described species, *Acineta pyriformis* Stokes, also possesses this feature and has been included in the genus *Veracineta* for the first time.

Diagnosis of *Veracineta*

Freshwater or marine loricate suctorians whose outline is pyriform and oval in cross-section. Actinophores absent. Capitate tentacles arranged in a single apical fascicle protruding through an oval apical aperture. A stalk attaches the suctorian to either copepods or to aquatic plants. Macronucleus oval to elongate. Single bud produced, presumably endogenously although this has not yet been reported fully, with 4 oblique ciliary rows. If budding is later observed to be external then the genus should be included in *Paracineta* Collin, 1911.

Key to the species of *Veracineta*

1 Marine, ectocommensal on copepods . . . . ***V. tisbei***
Freshwater, growing on aquatic plants . . . . ***V. pyriformis***

Species descriptions

Veracineta tisbei (Guilcher, 1950) Jankowski, 1978

Acineta tisbei Guilcher, 1950

Description (Fig. 65). This the type species is a rather small (lorica about 25 µm long), pyriform suctorian whose apex is wider than its base. The cell only occupies the anterior quarter of the lorica which is oval in cross-section. The lorica is pierced apically by an oval aperture through which the single apical fascicle of capitate tentacles protrude. The lorica is mounted on a stalk and attached via a circular plate to the cephalothorax of the copepod *Tisbe furcata* Baird. The macronucleus is oval to elongate. The actual process of budding has not been described but is presumed to be endogenous. However the buds have been observed and described in some detail. Indeed, Guilcher (1950) reported that, in most specimens, the buds lay inside and completely occupied the lorica (Fig. 65B) whilst few adults were observed. Buds have 4 oblique ciliary girdles which originate at the anterior and an apical scopula region composed of several kinetosomes grouped together.

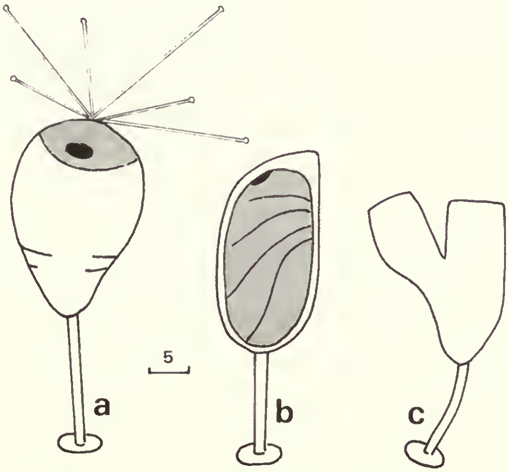

Fig. 65 *Veracineta tisbei*, after Guilcher, 1950 (called *Acineta tisbei*).

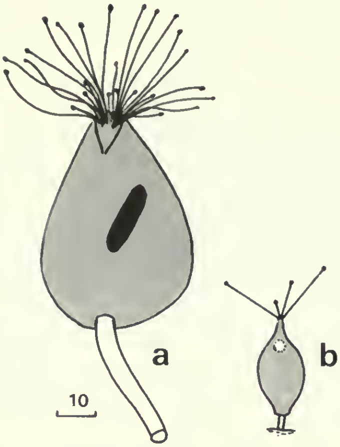

Fig. 66 *Veracineta pyriformis*: (a) after Gassovsky, 1916 (called *Acineta pyriformis*); (b) after Stokes, 1891 (called *Acineta pyriformis*).

Veracineta pyriformis (Stokes, 1891) n. comb.

Acineta pyriformis Stokes, 1891

DESCRIPTION (Fig. 66). This species has been described on two occasions (Stokes, 1891; Gassovsky, 1916) and the descriptions differ from each other in some respects that might reflect different ages of the specimens concerned. It is a small (23–60 µm long), loricate, freshwater suctorian that is approximately pyriform in outline with the base usually being broader than the apex. The cell completely fills the lorica and a single apical fascicle of capitate tentacles protrude through the oval aperture. Tentacle numbers vary from few to many, 4–25, and stalk length varies too, 1/4–2/3 lorica length. The animal attaches itself to aquatic plants including the alga *Cladophora* sp. The macronucleus is oval to elongate and there is a single anteriorly located contractile vacuole.

References*

Alder, J. 1851. An account of three new species of Animalcules. *Annals and Magazine of Natural History* **7** (Ser. 2): 426–427.

Allgén, C. 1952. Uber zwei neue antarktische Suctorien aus dem Graham Land. *Kungliga Fysiografiska Sallskapets i Lund. Forhandlingar.* **21:** 173–176.

Allman, G. J. 1875. Recent progress in our knowledge of the Ciliate Infusoria. *Monthly Microscopical Journal* **15:** 170–191.

Batisse, A. 1975. Propositions pour une nouvelle systématique des Acinétiens (Ciliophora, Kinetofragminophora, Suctorida). *Compte Rendu Hebdomadaire des Séances de l'Academie des Sciences, Paris* (Ser. D) **280:** 1797–1800.

Bory, St. Vincent de. 1825. *Encyclopedie Methodique. Zoologie. Histoire Naturelle des Zoophytes, ou Animaux Rayonnes.* pp. 819, Paris, Agasse.

Bütschli, O. 1887–1889. Protozoa. Abt III. Infusoria und System der Radiolaria. *In* Bronn, H. G. (Ed.), *Klassen und Ordnung des Thiersreichs* Vol. 1, pp. 1098–2035. Leipzig, C. F. Winter.

Calkins, G. N. 1902. Marine protozoa from Woods Hole. *Bulletin of the United States Fish Commission, Washington* **21**(yr 1901): 413–468.

Claparède, E. & Lachmann, J. 1859. Études sur les infusoires et les rhizopodes. *Mémoires de l'Institut National Genèvois, Genève* **6** (yr 1858): 261–482.

*NOTE: The author was unaware of the important paper by Jankowski (*Trudy zool. Inst. Leningr.* 1981, **107:** 80–115) until after the submission of this manuscript.

Collin, B. 1909. Diagnoses préliminaires d'Acinétiens nouveaux ou mal connus. *Compte Rendu Hebdomadaire des Scéances de l'Academie des Sciences, Paris* **149:** 1094–1095.

—— 1911. Étude monographique sur les Acinétiens I. Recherches expérimentales sur l'étendue des variations et les facteurs tératogènes. *Archives de Zoologie Expérimentale et Génerale, Paris* **8:** 421–497.

—— 1912. Étude monographique sur les Acinétiens II. Morphologie, Physiologie, Systématique. *Archives de Zoologie Expérimentale et Génerale, Paris* **51:** 1–457.

Corliss, J. O. 1979 .*The Ciliated Protozoa: Characterization, Classification and Guide to the Literature,* 2nd edition, Pergamon Press, Oxford, 455 pp.

Curds, C. R. 1982. *British and other freshwater ciliated protozoa. Part 1. Ciliophora: Kinetofragminophora.* Synopsis of the British Fauna (NS), **22:** pp. 387, London, Linnean Society.

Daday, E. von 1910. Die SüsswasserMikrofauna Deutsch-Ost-Afrikas. *Zoologica. Stuttgart* **59** (Bd. 23, Lfg 1–5): 1–314.

Daday, J. 1907. Adatok Német-Kelet-Afrika édesvízi mikrofaunájának ismeretéhez. *Matermatikai es Természettudomayi Ertesito, Budapest* **25:** 402–420.

Delamare Deboutville, Cl. & Chappuis, P. A. 1956. Présence d'un acinétien sur un Microcerberinae des eaux souterraines du Sahara Occidental. *Notes Biospéologique, Paris* **11** (2): 123–126.

Dons, C. 1918. Neue marine Ciliaten und Suctorien. *Tromsø Museums Aarshrifter* **38–39** (yr 1915–16): 75–100.

—— 1928. Neue und wenig bekannte Protozoen. *Kongelige Norske Videnskabernes Selskabs Skrifter* **7** (yr 1927): 1–17.

Ehrenberg, C. G. 1833. Dritter Beiträg zur Erkenntnis grosser Organisation in der Richtung des Kleinsten Raumes. *Abhandlungen der Akademie der Wissenschaften der DDR. Berlin.* yr. **1835:** 145–336.

—— 1838. *Die Infusionsthierchen als Volkommene Organismen.* 612 pp. Leipzig.

Entz, G. 1902. Nehany Patagoniae veglenyröl. *Matematekai es Természettudomanyi Ertesito, Budapest* **20:** 442–4369.

Fraipont, T. 1878. Recherches sur les Acinétiens de la côte d'Ostende. *Bulletin de l'Academie Royale de Belgique* **44:** 770–814.

Gajewskaja, N. 1933. Zur Oekologie, Morphologie und Systematik der Infusorien des Baikalsees. *Zoologica, Stuttgart* **32:** 1–298.

Gassovsky, G. N. 1916. (On the infusorian fauna of the Gulf of Kota and its environs—in Russian). *Trudy̆ Imperatorskago Sankt-Peterburgskago Obshchestva Estestvoispytatelei S.-Peterburg* **45** (4): 137–209. English summary pp. 210–215.

Goodrich, J. P. & Jahn, T. L. 1943. Epizoic suctoria (Protozoa) from turtles. *Transactions of the American Microscopical Society* **62:** 245–253.

Gourret, P. & Roeser, P. 1886. Les Protozoaires du Vieux-Port de Marseille. *Archives de Zoologie Expérimentale et Génerale, Paris* **4:** 443–534.

Gruber, A. 1884. Die Protozoen des Hafens von Genua. *Nova Acta Leopoldina, Halle a.S.* **46:** 475–539.

Guilcher, Y. 1950. Sur quelques Acinétiens nouveaux ectoparasites de Copépodes Harpacticides. *Archives de Zoologie Expérimentale et Génerale, Paris* **87** (*Notes et Revue* No. 1): 24–30.

—— 1951. Contributions à l'étudé des ciliés gemmipares, Chonotriches et Tentaculifères. *Annales des Sciences Naturelles, Paris* (Zool) **13:** 33–132.

Hadži, J. 1940. Neue symphorische Suktorien: *Spelaeophrya polypoides* sp.n., *Spelaeophrya lacustris* sp. n., *Acineta karamani* sp.n., und deren Entwicklungskreise. *Bulletin de l'Academie des Sciences Mathematiques et Naturelles, Belgrade* **6B:** 39–56.

Hertwig, R. 1875. Ueber *Podophrya gemmipara* nebst Bemerkungen zur Bau und zur systematischen Stellung der Acinetien. *Morphologisches Jahrbuch, Leipzig* **1:** 20–82.

Holm, F. 1925. Ueber die Suktorien in der Elbe bei Hamburg ind ihre Lebensbdungungen. *Archive fur Hydrobiologie, Stuttgart* **4:** 389–440.

Jankowski, A. V. 1967. (New genera of tentacled Infusoria (Suctoria)—in Russian). *Materialy̆ V Konmferentsii uch Moldavii Zoologicheskii* p. 35: 6.

—— 1975. A conspectus of the new system of subphyllum Ciliophora Doflein, 1901. *In* Balashov, U. S. (Ed.) *Account of Scientific Sessions on Results of Scientific Work Year 1974: Abstracts of Reports. Tezisy Doklady̆ Zoolologeskii Instakademii Nauk SSR* pp. 26–27.

—— 1978. (Phylogeny and divergence of suctorians—in Russian). *Doklady̆ Akademii Nauk SSR* **242** (2): 493–496. English translation *Dokladȳ (Proceedings) of the Academy of Sciences of the USSR (Biol. Sci)* **242** (1–6) (yr 1979): 527–529.

Kahl, A. 1934. Suctoria *In* Grimp, G. & Wagler, E. (Eds.) *Die Tierwelt der Nord und Ostsee* Bd. **1.** (Teil II c5): 184–226.

Kellicott, D. S. 1885. Freshwater Infusoria. *Proceedings of the American Microscopical Society* **8:** 38–47.

Kent, W. S. 1880–1882. *A Manual of the Infusoria* vols **I–III:** pp. 913, London, David Bogue.

Keppen, N. 1888. Observations on the tentaculiferous Infusoria I. *Acineta pappilifera* nov.sp. *Zapiski Novorossiiskago Obshchstva Estestvoispytatelei, Odessa* **13:** 1–79.

Kormos, J. & Kormos, K. 1958. Determination in der Entwicklung der Suctorien II. Neue untersuchungen uber determinativen zusammenhang zwischen der schwarmerbildung und der metamorphose. *Acta Biologica Academiae Scientiarium Hungaricae, Budapest* **9:** 25–45.

Lachmann, J. 1859. Sitzungsberichte vom 6 Juli 1859. *Verhandlungen des Naturhistorischen Vereins der Preussischen Rhienlande und Westfalens, Bonn* **16:** 91–94.

López-Ochoterena, E. 1963. Protozarios ciliados de Mexico 9. Notas sobre la morfologia de *Acineta tuberosa* Ehrenberg, 1833 (Protozoa, Suctorida). *Revista Latinoamericana de Microbiologia* **6:** 77–83.

Maskell, W. M. 1886. On the freshwater Infusoria of the Wellington District. *Transactions and Proceedings of the New Zealand Institute* **19:** 49–61.

—— 1887. On the freshwater Infusoria of the Wellington District. *Transactions and Proceedings of the New Zealand Institute* **20:** 4–19.

Matthes, D. 1954. Suktorienstudien I. Beiträg zur Kenntnis der Gattung *Discophrya* Lachmann. *Archiv für Prostistenkunde* **99:** 187–226.

—— 1956. Suktorienstudien VIII. *Thecacineta calic* (Schroder, 1907) (Thecacinetidae nov.fam.) und ihre Fortpflanzung durch Vermoid-Schwarmer. *Archiv. für Prostistenkunde* **101:** 477–528.

Maupas, E. 1881. Contribution à l'étude des Acinétiens. *Archives de Zoologie Expérimentale et Génerale, Paris* **9:** 299–368.

Muller, O. F. 1786. *Animalcula Infusoria Fluviatilia et Marina.* 367 pp. Havniae et Lipsiae.

Pallas, P. S. 1766. *Elenchus Zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones* 451 pp. Hagae Comitis.

Penard, E. 1920. Étude sur les Infusoires Tentaculifères. *Mémoires de la Societé de Physique et d'Histoire Naturelle de Genève* **39:** 131–227.

Precht, H. 1935. Epizoen der Kieler Bucht. *Nova Acta Leopoldina, Halle a.S.* **3:** 405–474.

Pritchard, A. 1852. *A history of infusorial animalcules, living and fossil,* pp. 704. London, Whittaker & Co.

Prowasek, S. von 1900. Beobachtungen an Seeswasser-Acineten. *Naturwissenschaftliche Wochenschrift* **15** (38): 450–451.

Rieder, J. 1936. Beiträg zur Kenntnis der Süsswasser-Suktorien und Revision der Schweizer Suktorien-Fauna. *Revue Suisse de Zoologie* **43:** 359–395.

Robin, C. 1879. Mémoire sur la structure et la reproduction de quelques infusoires tentaculés, suceurs et flagellés. *Journal de l'Anatomie et de la Physiologie Normales et Patholologiques de l'Homme et des Animaux, Paris* **15:** 592–683.

Sand, R. 1899–1901. Étude monographique sur le groupe des Infusoires Tentaculifères. *Annales de la Societe Belge de Microscopie* **24:** 57–189, **25:** 1–204.

Schulz, E. 1932. Beitrage zur Kenntnis mariner Suctorien. *Zoologischer Anzeiger, Leipzig* **97:** 289–292.

—— 1933. Beitrage zur Kenntnis mariner Suctorien. *Zoologischer Anzeiger, Leipzig* **103:** 327–329.

Stokes, A. C. 1885*a*. On some new Infusoria from American fresh water. *Annals and Magazine of Natural History* **15:** 437–449.

—— 1885*b*. Notices of new freshwater Infusoria. *American Monthly Microscopical Journal, New York* **6:** 183–190.

—— 1886. Notices of new freshwater Infusoria. *Proceedings of the American Philosophical Society* **23:** 562–568.

—— 1891. Notes of new Infusoria from the fresh waters of the United States. *Journal of the Royal Microscopical Society* **1891:** 700–704.

—— 1894. Notices of presumably undescribed Infusoria. *Proceedings of the American Philosophical Society* **33:** 338–345.

Swarczewsky, B. 1928. Zur Kenntnis der Baikalprotistenfauna. Die an Baikalgammariden lebenden Infusorien. IV. Acinetidae. *Archiv. fur Prostistenkunde* **63:** 362–409.

Wailes, G. H. 1928. Freshwater and marine protozoa from British Columbia with descriptions of new species. *Museum and Art Notes, Vancouver* **3:** 25–37.

—— 1943. Protozoa et Suctoria. *Canadian Pacific Fauna* **1:** 1–46.

Wang, C. C. & Nie, D. 1933. A survey of the marine protozoa of Amoy. *Contributions from the Biological Laboratory of the Science Society of China, Nanking* **8** (yr 1932): 285–385.

Wright, T. S. 1858. Description of new protozoa. *Edinburgh New Philosophical Journal* **7:** 276–281.

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C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post) Co-published by British Museum (Natural History) and Oxford University Press.

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The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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Titles to be published in Volume 48

Miscellanea

A revision of the Suctoria (Ciliophora, Kinetoframinophora) 1. *Acineta* and its morphological relatives. By Colin R. Curds

Notes on the anatomy and phyletic relationships of *Hemichromis* Peters, 1858. By Peter Humphry Greenwood

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Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

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Zoology series Vol 48 No 3 30 May 1985

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World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

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The Zoology Series is edited in the Museum's Department of Zoology

Keeper of Zoology : Mr J. F. Peake
Editor of Bulletin : Dr C. R. Curds
Assistant Editor : Mr C. G. Ogden

ISBN 0 565 05013 3
ISSN 0007-1498

Zoology series
Vol **48** No. 3 pp 131-171

British Museum (Natural History)
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Introduction

Students of cichlid taxonomy have long speculated on the phyletic relationships of the endemic African genus *Hemichromis* Peters (1858), a taxon which superficially appears quite distinct from other African cichlids, and in some respects is more like certain Neotropical members of the family.

Early views on the affinities of *Hemichromis*, albeit more probably statements of phenetic resemblance than phyletic affinity, are those of Pellegrin (1903 : 252) and Sauvage (1907, 1910). Pellegrin considered *Hemichromis* to be close to, and differing little from, the South American genus *Acara* (probably to be interpreted as *Aequidens)*; Sauvage, however, first allied *Hemichromis* with his fossil, *Palaeochromis*, from the Eocene of Africa, and later thought that genus to be intermediate between *Hemichromis* and *Acara*.

Entirely African affinities for the genus were implied by Regan (1922) who considered *Hemichromis* and *Haplochromis* (as then broadly conceived) to be very closely related.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(3): 131–171 Issued 30 May 1985

There, at least in print, matters rested until fifty years later Loiselle & Welcomme (1972) postulated *Hemichromis* as the nearest relative of their newly discovered genus *Thysia* from West Africa; these authors also suggested that *Hemichromis* might be an unnatural taxon, an idea apparently abandoned by the senior author a few years later (Loiselle, 1979). More recently, Van Couvering (1982) recognized *Hemichromis* as constituting the plesiomorph sister group of an assemblage comprising *Pseudocrenilabrus* and *Haplochromis,* the latter again broadly conceived as in Regan's time.

Only Loiselle and Welcomme amongst these authors provided anything approaching a detailed reasoning for their conclusions. None based their views on a wide-ranging anatomical comparison with other taxa from Africa or those from the Neotropics. In fact, remarkably little is known about the anatomy of *Hemichromis.* The only source of information is Vandewalle's (1971:268–272) not especially detailed or widely comparative account of the cephalic skeleton and musculature in *H. fasciatus.*

One of the objects of the present paper is to take a fresh look at the phylogenetic relationship of *Hemichromis* using information derived from more detailed anatomical studies, by extending the comparative basis to include not only more African taxa but also Madagascan and Neotropical species, and by using, in the final analysis of its relationships, only features which, as far as can be established, are derived ones.

Another object of this paper is an attempt to assess whether or not *Hemichromis* should be ranked as one of the 'primitive' African cichlids, a status which it has been accorded by two recent workers, Cichocki (1976) and Van Couvering (1982).

The results of this investigation are, in one respect, disappointing. On the positive side, *Hemichromis* can be shown to be a member of the African cichlid assemblage, and that amongst that assemblage it is not an entirely primitive taxon; indeed it possesses several unique derived features, and shares many other apomorphies with various African and Neotropical species. The disappointment stems from the fact that a presumed sister group for the genus can only be recognized on a synapomorphy that could be considered equivocal.

Materials and methods

The entire collection of BMNH cichlid dry skeletons and alizarin preparations was examined. Thus, as far as African taxa are concerned a representative of virtually every genus was examined, and in the case of the larger lakes and rivers, several species of a genus were studied. In preparing the skeletal collections of Lake Victoria and Lake Edward haplochromines I had made notes on various anatomical features; these data were used in this paper, and so obviated the need for additional dissections. However, dissections were made on various taxa from Lakes Malawi, Tanganyika and Turkana, and on species from rivers and smaller water bodies. These are listed below.

Much of the information on Neotropical species was taken from Cichocki (1976), but several dry skeletons and alizarin preparations were examined, and dissections were carried out on others. These too are listed below, as are the various outgroup taxa studied.

The notation (1) or (2), which precedes non-*Hemichromis* species listed under the sections 'African material: Dissections' and in the Neotropical, Asian and Madagascan skeleton and dissected material sections, indicates the nature of the ethmopalatine articulation. (1) means a single, anterior articulation between the palatine and the lateral ethmoid; (2) indicates a double articulation: anteriorly as described above, and posteriorly between the palatine and a facet on the ventral face of the lateral ethmoid (see pp. 137–140).

Materials

Hemichromis fasciatus

Dissections: 1976.11.12:138–141; 1953.4.28:243–244.
Alizarin preparations: 1976.11.12:135–137; 1952.4.13:4218–4231.
Dry skeletons: 1953.4.28:243–248; 1883.4.19:15.

Hemichromis bimaculatus

Dissections: 1896.3.9:6–10
Alizarin preparations: 1982.4.13:4180–4186.
Dry skeletons: 1982.4.13:4180–4186; 1865.5.3:45.

The nature of the ethmopalatine joint, and the distribution of ethmomaxillary and ethmopalatine ligaments, in species other than *H. fasciatus* and *H. bimaculatus* were studied from dissections on: *H. guttatus* 1906.5.28:66–67; *H. frempongi* 1917.4.20:27–28; 1942.12.30:1–10; *H. cerasogaster* 1979.3.5:358–9; 1899.11.27:67–86; *H. paynei* 1950.9.22:51–55; *H. elongatus* MRAC 172736–172750; *H. lifalili* AMNH 19704; *H. letourneauxi* 1907.12.2:2989–3013; *H. stellifer* AMNH 16864 (4 paratypes).

All *Hemichromis* specimens were chosen from material examined and identified by Loiselle (1979).

African species
Dissections:
(2) *Astatotilapia flaviijosephi* 1983.7.6:27–33
(2) *Astatotilapia burtoni* 1950.4.1:2176–2200
(2) *Astatotilapia 'bloyeti* complex' 1958.12.5:76–87
(2) *Aulonocara nyassae* 1935.6.14:2251–2255
(2) *Aulonocranus dewindti* 1969.9.30:4269–4641
(2) *Bathybates fasciatus* 1960.9.30:6018–6020
(1+2) *Bathybates ferox* 1960.9.30:5952–5957
(1) *Bathybates graueri* 1960.9.30:6274–6283
(2) *Bathybates horni* 1960.9.30:6284–6286
(1) *Bathybates minor* 1950.4.1:5708–5744
(1) *Bathybates vittatus* 1960.9.30:6293–6295
(2) *Chilotilapia rhoadesi* 1935.6.14:2103–2112
(2) *Chromidotilapia finleyi* 1979.2.23:18–19
(2) *Chromidotilapia guentheri* 1973.5.14:615–626; 1930.3.24.25–26
(2) *Corematodus shiranus* 1935.6.14:2008–2011
(2) *Ctenochromis polli* 1964.5.28:1–2
(2) *Cynotilapia afra* 1965.10.25:6–19
(2) *Cyphotilapia frontosus* 1982.4.13:4737
(2) *Cyrtocara eucinostomus* 1962.10.18:1–10
(2) *Cyrtocara chrysonotus* 1935.6.14:1823–1832
(2) *Eretmodus cyanostictus* 1950.4.1:5171–5183
(2) *Genyochromis mento* 1965.10.26:24–29
(2) *Gephyrochromis lawsi* 1956.9.4:18
(2) *Grammatotria lemairei* 1950.4.1:3758–3785
(2) *Hemibates stenosoma* 1961.11.22:999–1005
(2) *Hemitilapia oxyrhynchus* 1936.5.14:2142–2145
(1) *Konia dikume* 1973.5.14:643–649
(2) *Labeotropheus fuelleborni* 1935.6.14:205–274
(2) *Lamprologus cunningtoni* 1950.4.1:6677–6694
(2) *Lamprologus moori* 1950.4.1:6586–6603
(2) *Leptotilapia irvinea* 1974.1.2:225–228
(2) *Lethrinops lethrinus* 1930.1.31:144–149
(2) *Lichnochromis acuticeps* 1956.6.12:20–22
(2) *Lobochilotes labiatus* 1950.4.1:616–639
(1) *Myaka myaka* 1973.5.14:719–723
(2) *Nanochromis nudiceps* unregistered *ex* Stanley Pool
(2) *Oreochromis niloticus* 1907.12.2:3351–3353
(2) *Oreochromis tanganicae* 1919.1.16:126
(2) *Oreochromis variabilis* 1958.12.4:1–7
(2) *Pelmatochromis buettikoferi* 1911.5.31:45–48
(2) *Pelmatochromis kribensis* 1952.8.26:7–8
(2) *Pelvicachromis pulcher* 1915.4.13:45–47
(2) *Pelvicachromis roloffi* 1972.9.27:78–85

(2) *Petrotilapia tridentiger* 1965.10.26:30–36
(2) *Pseudocrenilabrus philander dispersus* 1935.3.20:4–9
(1) *Pterochromis congicus* 1901.12.21:77
(2) *Pungu maclareni* 1973.5.14:769
(2) *Rhamphochromis longiceps* 1935.6.14:2172
(2) *Sarotherodon caroli* 1973.5.14:769
(1) *Sarotherodon linelli* 1973.5.14:861–872
(2) *Sarotherodon melanotheron* 1971.8.13:13–14
(2) *Serranochromis angusticeps* 1932.12.16:538–540
(2) *Steatocranus casuarius* 1977.1.11:274–410
(2) *Stomatepia mariae* 1973.5.14:948–988
(1) *Teleogramma gracilis* 1976.5.21:88–97
(2) *Thoracochromis albertianus* 1929.1.24:318–322
(2) *Thoracochromis buysi* unregistered. Cunene river
(2) *Thoracochromis macconneli* 1973 11.13:38–58
(2) *Thysia ansorgii* 1977.11.8:436–455
(2) *Tilapia ruweti* 1969.3.28:1–6
(2) *Tilapia sparrmani* 1966.7.20:12–13
(2) *Trematocara unimaculatum* 1961.11.22:529–537
(2) *Tristramella simonis* 1968.12.13:55–65
(2) *Xenotilapia melanogenys* 1950.4.1:3944–3978

Genus *incertae sedis:*
(2) *Pelmatochromis thomasi* 1914.12.9:9–11 (syntypes); 1981.8.17:22–41; 1981.6.19:119–121

Madagascan and Asian species
Dissections;
(2) *Ptychochromis oligacanthus* 1980.2.1:5–6; 1982.2.25:71–73
(1) *Paratilapia polleni* 1876.10.3:33; 1960.9.30:6274–6283
(1) *Paretroplus dami* 1969.2.7:1–3
(1) *Etroplus maculatus* 1958.6.10:69–74

Neotropical species
Dissections:
(2) *Acarichthys heckeli* 1925.10.28:398–402
(2) *Aequidens vittatus* 1973.2.7:1–9
(2) *Astronotus ocellatus* 1926.10.27:440–443
(1) *Batrachops reticulatus* 1968.9.26:327–328
(1) *Chaetobranchus flavescens* 1926.10.27:426–427
(1) *Cichla ocellaris* 1968.9.26:23–24
(1) *Cichlasoma motaguense* 1925.3.6:132–135
(2) *Crenicichla saxatilis* 1981. 6.9:1209–1210
(1) *Heterotilapia multispinosa* 1925.3.6:162–164
(1) *Microgeophagus ramirezi* 1952.7.30:6–7
(1) *Pterophyllum scalare* unregistered *ex* Zoo. Soc. London

Dry skeletons:
(1) *Acaronia nassa*
(1) *Aequidens tetramerus*
(1) *Cichla ocellaris*
(2) *Cichlasoma cyanoguttatum*
(1) *Cichlasoma facetum*
(1) *Cichlasoma motaguense*
(1) *Cichlasoma sieboldi*
(2) *Crenicichla johanna*
(1) *Geophagus braziliensis*
(1) *Geophagus jurupari*
(1) *Geophagus surinamensis*
(1) *Symphysodon discus*

Outgroups
Dissections:
Centropomidae: *Lates niloticus.*, Unregistered
Serranidae: *Serranus cabrilla* 1936.12.30:7–8
Percidae: *Perca fluviatilis* 1967.8.3:21–25
Labridae: *Halichoeres bivittatus* 1980.9.22:250–252
Pseudolabrus luculentus 1977.4.4:101–108
Pomacentridae: *Amphiprion ocellaris* 1984.1.18:185–187
Pomacentrus leucostictus 1933.10.12.41–50
Embiotocidae: *Cymatogaster aggregata* 1981.5.19:45–69
Embiotoca jacksoni 1981.5.19:5–6
Neoditrema nansonneli 1905.2.4:240–244

Abbreviations used in text figures

The scale bar in the figures is divided into millimetres.

A_{1-3}	Adductor mandibulae muscles 1–3
A_w	Adductor mandibulae muscle A_w
af hymd	Anterior facet for head of hyomandibula
ang art	Anguloarticular bone
apn	Aponeurosis
art s pb3	Articular surface of 3rd pharyngobranchial bone
art v lat pr	Surface for articulation with lateral process of the vomer
awn	Lateral awning area
bb 1–4	1st–4th basibranchial elements (4th is cartilaginous)
bh	Basihyal bone
boc	Basioccipital
boc f	Basioccipital facet for articulation with upper pharyngeal bones
bsph	Basisphenoid
cal	Calyx
cb 1–4	1st–4th ceratobranchials
cl	Cleithrum
cor	Coracoid
cts	Connective tissue sheet
d cart	Dorsal accessory cartilage
den	Dentary
ect	Ectopterygoid
entp	Entopterygoid
epo	Epioccipital
epb 1–4	1st–4th epibranchials
epb 4 br	Bony ridge on 4th epibranchial
exo	Exoccipital
f hym	Foramen for branch of facial nerve
f oln	Foramen for olfactory nerve
fr	Frontal
fz	Frayed zone
ga II–IV	Gill arches I–IV
hb 1–3	1st–3rd hypobranchials
hym	Hyomandibula
hymd sh	Hyomandibulad pit
hypp	Hypurapophysis
ic	Intercalar
inth	Interhyal
iop	Interoperculum

lac fac	Facet for lachrymal (1st infraorbital) bone
lat comm	Lateral commissure
lat pr vom	Lateral process of vomer
l eth	Lateral ethmoid
lphyj	Lower pharyngeal bone
m aap	Adductor arcus palatini muscle
m add op	Adductor operculi muscle
m add 5	Adductor 5 muscle
m c-p^2	Cranio-pharyngobranchialis 2 muscle
m dilop	Dilatator operculi muscle
m im	Intermandibularis muscle
m lap	Levator arcus palatini muscle
m le 1–4	Levator externus muscle 1–4
m lev post	Levator posterior muscle
m li 1&2	Levator internus muscles 1 & 2
m lop	Levator operculi muscles
m obl d ant	Obliquus dorsalis anterior muscle
m obl d post^1	Obliquus dorsalis posterior muscle, pars medialis
m obl d post^2	Obliquus dorsalis posterior muscle, pars lateralis
m pro pect	Protractor pectoralis muscle
m rab	Retractor arcuum branchialium muscle
m sph oes	Sphincter oesophagi muscles
m tdp	Transversus dorsalis posterior muscle
m t-e2	Transversus epibranchialis 2 muscle
max	Maxilla
meth	Mesethmoid
metp	Metapterygoid
metp r	Ridge on metapterygoid
mxhd	Maxillary head of palatine bone
ncc	Neurocranial condyle of premaxilla
oes	Oesophagus
op	Operculum
pal	Palatine
pal-lac lig	Palato-lachrymal ligament (cut)
pal-pal lig	Palato-palatine ligament
pal-vom lig	Palato-vomerine ligament
pal vom pr	Vomerine process of palatine
par	Parietal
pc 1–2	First and second postcleithra
p f hymd	Posterior facet for head of hyomandibula
phyb 1–3	Pharyngobranchials 1–3
pop	Preoperculum
pop-retar lig	Preopercular-retroarticular ligament
pr	Anterior process on 2nd postcleithrum
pro	Prootic
psph	Parasphenoid
psph f	Parasphenoid facet for articulation with upper pharyngeal bones
pto	Pterotic
pts	Pterosphenoid
q	Quadrate
qr r	Quadrangular region of 4th epibranchial bone
ra	Retroarticular
r cart	Rostral cartilage
rdg	Ridge
rds	Pectoral fin radials

r ect	Recess in ectopterygoid bone for the *adductor arcus palatini* muscle
rost f	Rostral fenestra
r pal	Recess in palatine bone for the *adductor arcus palatini* muscles
sc	Scapula
sdl	Saddle
shr	Shank ridge
soc	Supraoccipital
socc	Supraoccipital crest
sop	Suboperculum
sp	Shank spine on 4th epibranchial bone
sph	Sphenotic
sut	Suture between anterior flange of hyomandibula and metapterygoid
symp	Symplectic
t A_1a	Tendon from muscle A_1 to maxilla
t A_1b	Tendon from muscle A_1 to lower jaw
t A_w	Tendon from muscle A_w
tem	Triangular prominence on maxilla
t-l pal proc	Thumb-like process of palatine (for articulation with anterior face of lateral ethmoid)
trf	Triangular fossa in frontals
up 4	4th upper pharyngeal tooth plate
v cart	Ventral accessory cartilage
vom	Vomer
vom c	Vomerine crest
vom fs	Vomerine fossa
vp pal	Vomerine process of palatine

Notes on the osteology and anatomy of *Hemichromis*

Apart from certain features studied by Cichocki (1976), and a few neurocranial characters noted by Stiassny (1982) and Van Couvering (1982), the only osteological and myological account of *Hemichromis* is that of Vandewalle (1971). That account is somewhat superficial, took into account only *H. fasciatus*, and overlooked most of the major anatomical peculiarities of the genus.

The anatomical and osteological descriptions given below are also based primarily on *H. fasciatus*, type species of the genus. They are, however, supplemented by observations on *H. bimaculatus*, and where material permitted, on other species of the genus as well. One critical feature, the nature of the palatoethmoidal articulation, has been checked in ten of the species recognized by Loiselle (1979) in his species-level revision of the genus. No suitable material of *H. cristatus* was available for dissection, but the palatoethmoidal articulation in this species was checked, and confirmed, from radiographs.

Osteology

NEUROCRANIUM

The overall morphology of the neurocranium is shown in Figs 1 & 2, and calls for no further comments.

Ethmovomerine region (Figs 1 & 2). This region of the skull departs markedly from the condition found in all other cichlids examined. In large part these peculiarities are associated with the unusual and unique ethmopalatine articulatory system of *Hemichromis* (see pp 138–140). Since that system occurs in all species, most of the peculiarities occurring in this region of the skull in *H. fasciatus* and *H. bimaculatus* are probably present in every member of the genus.

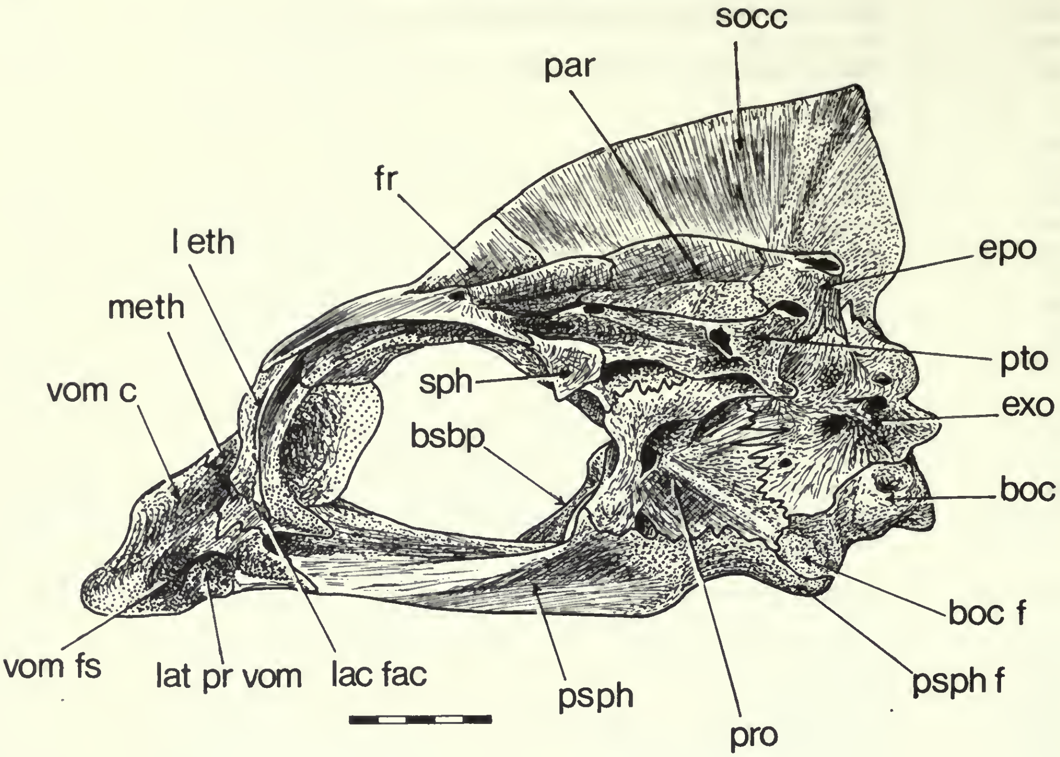

Fig. 1 *Hemichromis fasciatus*. Neurocranium, left lateral view (1953.4.28:243–4; 120 mm SL).

Over slightly more than the posterior half of its length, the dorsal surface of the *vomer* in *H. fasciatus* is considerably elevated to form a casket-like crest with a broad, slightly cambered upper surface. The crest is continuous with a similar median elevation of the *mesethmoid's* anterior half. The mesethmoid and the vomer have a deeply interdigitating sutural union. Immediately anterior to the suture, at least in dry skulls, a small area of the vomer's dorsal surface is incomplete (the rostral fenestra of Stiassny, 1981*a*:73). In freshly prepared skulls this ovoid hole is filled by a protruding cartilaginous plug.

A similar ethmovomerine crest is present in *H. bimaculatus*, but is relatively lower and less obvious than its counterpart in *H. fasciatus*.

In both species the tip of the vomer is bulbous and indented medially. A short distance behind the bulbous region, the ventrolateral margin of the vomer is produced, on each side, into a broad, near-triangular lateral process whose tip projects slightly beyond the lateral margins of the bulbous part (Figs 1–4). The anterior surface of the lateral process underlies, and articulates with, the vomerine process of the palatine (see p. 144; also Fig. 4). The gently rounded dorsal and posterior faces of the lateral process contact the ventral face of the palatine immediately behind the base of that bone's vomerine process.

As far as I can tell from an extensive survey of African and Neotropical cichlids, *Hemichromis* is unique in having this kind of vomerine support for, and articulation with, the palatine. In all other taxa the only vomeropalatine contact is through a simple, face-to-face joint between the articular head of the palatine's vomerine process (the palatine wing of Barel *et al*, 1976) and a facet on the lateral aspect of the vomer (the vomerine palatinad articulation of Barel *et al.* 1976).

Hemichromis fasciatus and *H. bimaculatus* do, however, have a second point of articulation between the vomer and palatine which is apparently homologous with the usual one in cichlids. It is effected through the tip of a well-developed process on the palatine inserting into a deep pit in the lateral wall of the vomer immediately above the base of the lateral vomerine process (see above). The pit in *Hemichromis* would seem to correspond to the vomerine fossa in other cichlids (see Stiassny, 1981*a*), and the process on the palatine with the palatine wing (*sensu* Barel *et al,* 1976). The most obvious difference between the two systems is that, in other cichlids, the vomerine palatinad articulation of Barel *et al* lies immediately anterior to the vomerine fossa, whereas in *Hemichromis* the articulation point lies within what appears to be the vomerine fossa.

All the cichlids I examined, apart from *Hemichromis,* have an articulation anteriorly between the lateral ethmoid and the palatine. Usually this is brought about by contact between a facet on the medial face of the palatine meeting a facet on the lateral aspect of the lateral ethmoid, near or overlapping its suture with the vomer (*ie* Stiassny's [1981*a*] ovoid fenestra; see also figs 1–3 in that paper). No such articulation occurs in any of the *Hemichromis* species I examined. Instead, there is an elaborate joint developed between the anterior face of the lateral ethmoid and the palatine; this will be described below.

In addition to the anterior contact between the lateral ethmoid and the palatine, there is, in the great majority of African cichlids examined, and in some but relatively fewer Neotropical species, a posterior ethmopalatine articulation as well (see lists in 'Materials' section, p. 132; also Cichocki, 1976). This posterior contact is between a short, drum-like facet on the ventral surface of the lateral ethmoid, and an elongate facet on the postero-dorsal surface of the palatine's posterior wing (the lateral ethmoid articulation facet of Barel *et al,* 1976). Generally the drum-like facet on the lateral ethmoid is situated near the posterior and median margins of that bone. No such posterior ethmopalatine articulation is present in *Hemichromis,* and there is no drum-like facet ventrally on the lateral ethmoid. Indeed, there is a relatively large gap between the palatine and that region of the skull.

Hemichromis does, however, have a different kind of ethmopalatine articulation, and one which has not been found in any other cichlid. The articulation (see Figs 3 & 4) is between an upwardly directed, transversely orientated process on the palatine (probably corresponding to Barel *et al*'s [1976] mesethmoidad process in *Astatotilapia elegans*) and the anterior face of the lateral ethmoid immediately below the foramen for the olfactory nerve (see Fig. 4). The lateral ethmoid facet has a complex form. Anteroventrally there is a well-defined, vertically aligned articular surface for the palatine process. Its rounded anterior face runs laterally almost at right angles to the skull's sagittal plane and extends from about the level of the ethmovomerine crest to the point where the lateral ethmoid is produced downwards to form the prefrontal margin of the orbit. Immediately behind this part of the facet the ethmoid is formed into a second, but horizontally aligned articulatory surface. It lies in the floor of a deep and broad pit on the posterior wall of which the foramen for the olfactory nerve is situated. The medial wall of the pit is formed by the mesethmoid, but its floor, lateral wall and posterior face are formed by the lateral ethmoid. This facet, too, is involved in articulation with the palatine process (see p. 143 below).

There are some slight interspecific differences in the morphology of the ethmopalatine articulation in *Hemichromis.* The ethmoid pit and its articulatory surfaces are, however, always present but, as in *H. bimaculatus,* the horizontal component of the ethmoid facet may be better defined than the vertical one.

Neither *H. fasciatus* nor *H. bimaculatus* has an ovoid fenestra (see above). This cartilage-filled gap between the lateral ethmoid and the vomer was somewhat more accurately designated by Barel *et al* (1976) as the mesethmoid-palatine facet, since it serves, in the majority of cichlids, as the anterior point of articulation between the palatine and the ethmoid (or ethmovomerine bloc if the facet, as it often does, spans part of the suture between the vomer and lateral ethmoid).

That the facet (or fenestra) has disappeared in *Hemichromis* is not surprising when one considers the single type of ethmopalatine articulation present in that genus (see above, p. 137).

In short, *Hemicromis* differs from all other cichlids in having a double (and complex) palatovomerine articulation, and in having an elaborate articulation between the palatine and the anterior face of the lateral ethmoid. In other taxa this joint is a simple one between the palatine and the lateral ethmoid, or lateral ethmoid-vomer junction region. *Hemichromis* does, however, share with a number of other cichlids, especially Neotropical taxa, the loss of contact and hence articulation between the ventral face of the lateral ethmoid and the posterior wing of the palatine (see p. 166 for further discussion).

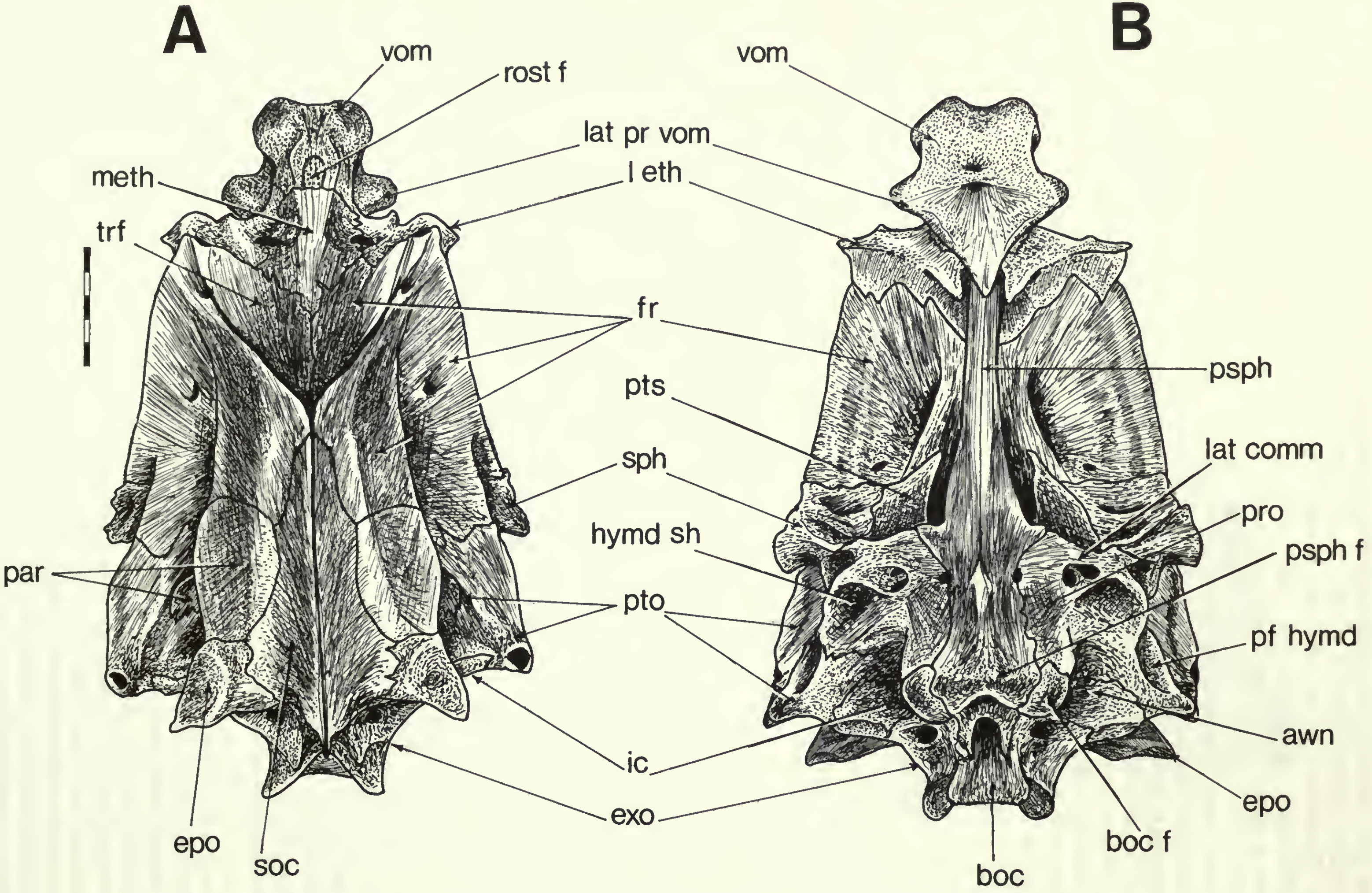
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Fig. 2 *Hemichromis fasciatus*. Neurocranium in: A. Dorsal view. B. Ventral view (1953.4.28: 243–4).

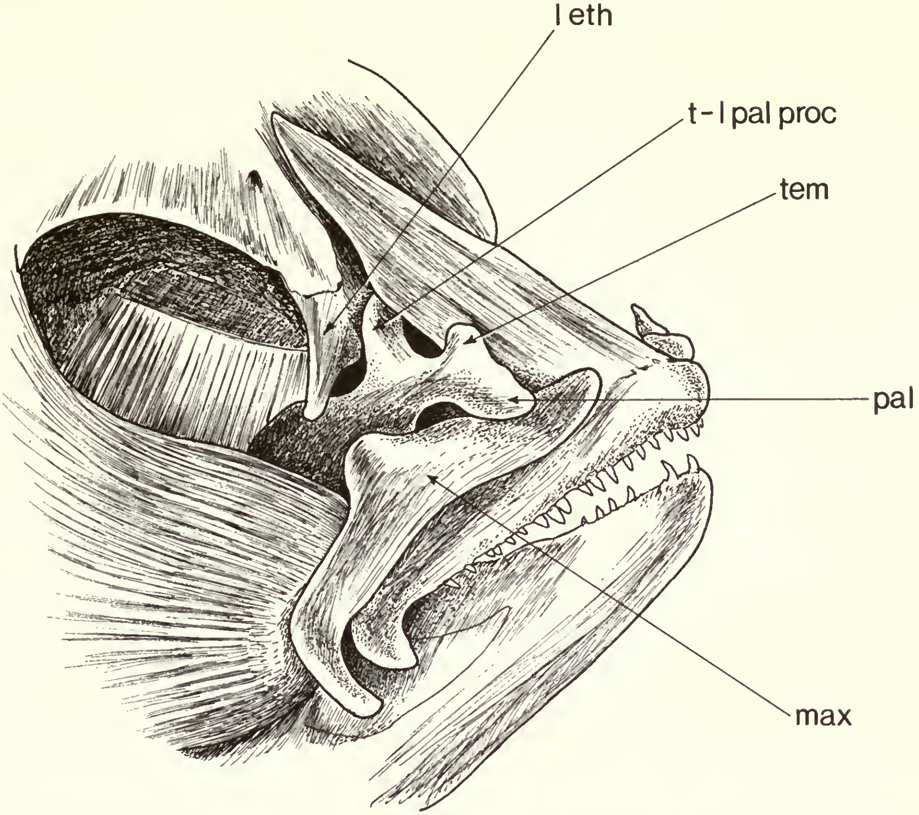


Fig. 3 *Hemichromis fasciatus*. Dissected snout, in dorso-anterior view, to show palato-ethmoid articulation.

Dorsicranium (Fig. 2A). As Vandewalle (1971) noted in *H. fasciatus* , there is a large, cartilage-filled area in the floor of the post-temporal fossa. It extends between the inner margins of the parietal, epioccipital and pterotic bones forming the fossa. Such a cartilage area, but of variable extent is present in all the cichlids I examined.

In *H. fasciatus* the mesethmoid and frontals meet along a broad, shallowly curved front which is continued laterally by the smooth overlap of lateral ethmoids and frontals. The fossa-like area lying between the anterior continuation of the frontals is broad and triangular, its apex is directed posteriorly, and it is deeply scoop-shaped in transverse section. The floor and walls of this triangular fossa (Fig. 2A) are formed by the frontals. Posteriorly its median wall is not continued backwards, as is usual in cichlids, as a pair of roofed, almost tubular cavities. These cavities are, however, present in *H. bimaculatus*. It would seem that the condition in *H. fasciatus* has resulted from the frontals failing to develop the medially directed and horizontal flanges which in other taxa, including *H. bimaculatus*, roof the median posterior extension of the fossa.

Vandewalle (1971) does not mention the absence of roofed extensions to the frontal fossa in *Hemichromis fasciatus*, but he does comment '. . . comme le signale Boulenger (1901), la crête supraoccipitale d'*Hemichromis* est *bifurquée* entres les orbites pour recevoir le processus ascendens des premaxillaire, . . . ' [italics added].

Boulenger's original observation and Vandewalle's confirmation of it are puzzling because neither the supraoccipital nor its crest extend anteriorly as far as the distal tips of the premaxillary ascending processes. I suspect that both authors misidentified, as part of the supraoccipital, the oblique, mediolaterally directed crests developed above the anterior part of the supraorbital lateral-line tubule on each frontal. These crests meet in the midline at the anterior tip of the

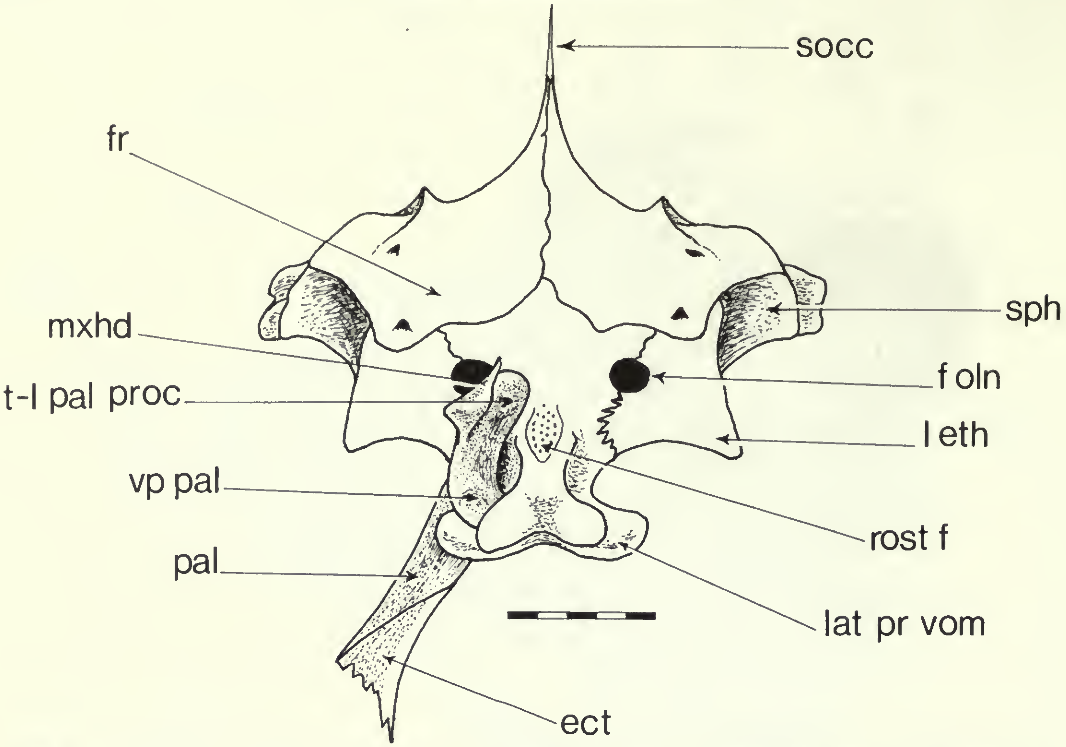


Fig. 4 *Hemichromis fasciatus.* Frontal view of neurocranium with right palatine in articulation, to show support of palatine by lateral process of vomer, and articulation of the thumb-like palatine process with the lateral ethmoid. (1953.4.28:243–4).

supraoccipital bone above the single coronal pore, and delimit the posterior margin of the scoop-like frontal fossa described earlier (Fig. 2A). The crests are homologues of the upswept anterior margin of the frontal area which, in other cichlids, roof the fossa's tunnel-like posterior extensions. Presumably it is the medial union of the crests anterior to the supraoccipital, and their apparent continuity with that bone, which misled Boulenger and Vandewalle into describing a bifurcate supraoccipital in *H. fasciatus.*

Otic region. The *pars jugularis* and *lateral commissure* are of the modal perciform type (Fig. 5). Van Couvering's figure (1982: fig. 5) of the *pars jugularis* in *H. bimaculatus* is slightly misleading since its posterior opening seems to be directed posteroventrally and not, as it actually is, posteriorly; this discrepancy probably is a result of the way (unspecified) in which the specimen was orientated.

A most noticeable departure of *Hemichromis* from the modal cichlid condition is seen in that part of the otic skull which Barel *et al* (1976) term the *hyomandibulad shell.* The hyomandibulad shell is that ventrally facing region of the prootic from which the greater part of the *levatores externi* muscles of the gill arches originates. In all cichlids I have examined, apart from *Hemichromis,* the shell is a flat or weakly concave area. In *Hemichromis,* however, it is a deep, dorsally directed indentation (Figs 1, 2 & 5) which, when seen from below, resembles a pyramidal pit. As far as I can tell, a deep, pit-like hyomandibulad shell is unique to *Hemichromis* amongst the cichlids, and does not occur elsewhere outside the family.

Immediately behind the pit, the area formed by the meeting of the pterotic, prootic, intercalar and exoccipital bones (Figs 2 & 5) was designated as the *lateral awning* by Barel *et al* (1976). In *Hemichromis,* especially in *H. fasciatus,* the awning is much more deeply concave than it is in other cichlids. Like the hyomandibulad pit, the lateral awning in *Hemichromis* is approximately triangular in outline and pyramidal in form. It is, however, a less distinctive departure from the

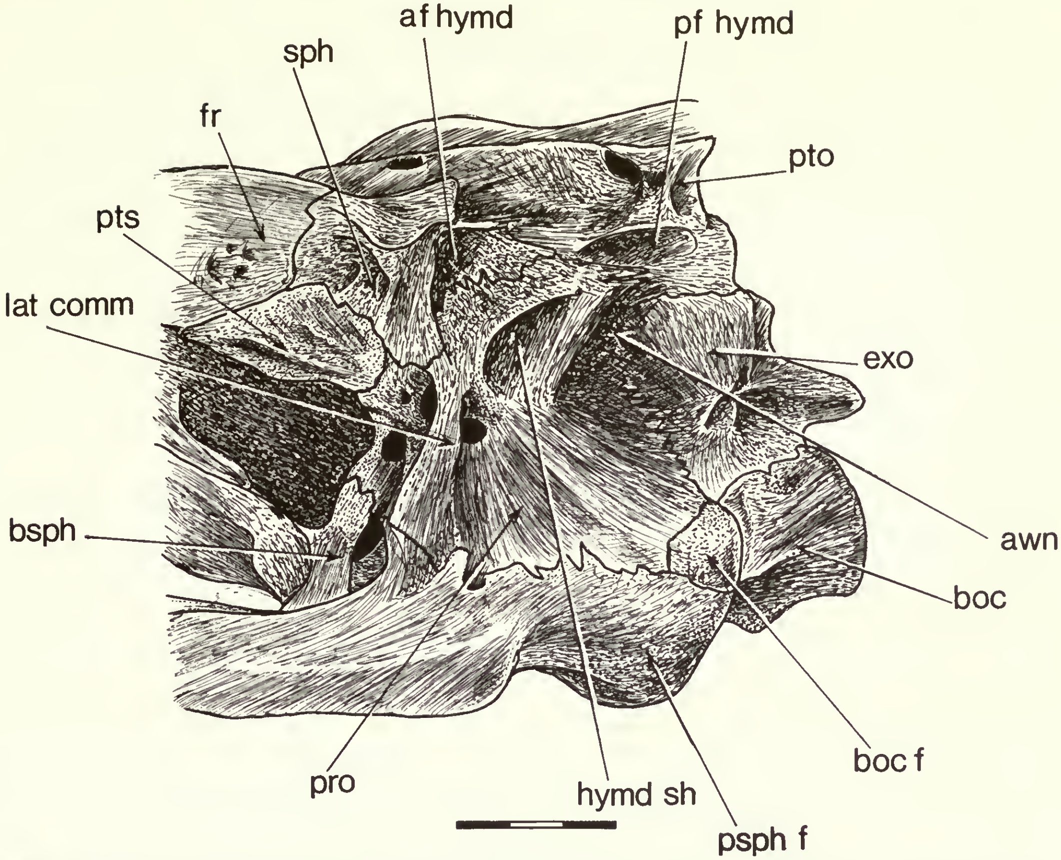


Fig. 5 *Hemichromis fasciatus*. Otic region of skull (left side) to show *pars jugularis* and its lateral commissure, and the form of the neurocranial apophysis for the upper pharyngeal bones. Specimen viewed from above and somewhat anteriorly, the transverse axis of the skull rotated to the right through *ca* 130° (1953.4.28:243–4).

usual cichlid condition, and is approached by the awning in, amongst other African species, *Pelmatochromis* and *Chromidotilapia,* and by the awning in some Neotropical taxa as well.

The intercalar is a large bone occupying somewhat more than the posterior half of the roof of the awning area.

Neurocranial apophysis for the upper pharyngeal bones. Structurally, the apophysis in *Hemichromis* is of the *Haplochromis*-type (Regan, 1920; also discussion in Greenwood, 1978), with a substantial basioccipital contribution on each side (Figs 1 & 5).

When the skull of *H. fasciatus* is viewed from behind, the ventral face of the apophysis is markedly convex, with most of its surface sloping upwards and outwards at an angle of about 45° to the horizontal. In sharp contrast, when the skull of *H. bimaculatus* is viewed in this way the apophyseal surface is virtually horizontal and thus like the modal condition in cichlids with a *Haplochromis*-type apophysis.

SUSPENSORIUM (Figs 6–8)

Palatoquadrate arch (Figs 6 & 7). Not surprisingly, in view of the unusual ethmopalatine articulation in *Hemichromis,* the *palatine* itself has a very characteristic form.

In *H. fasciatus* the bone is stout, with a short and wide maxillary process whose dorsomedial margin is produced into a wide-based triangular prominence. A little behind that prominence

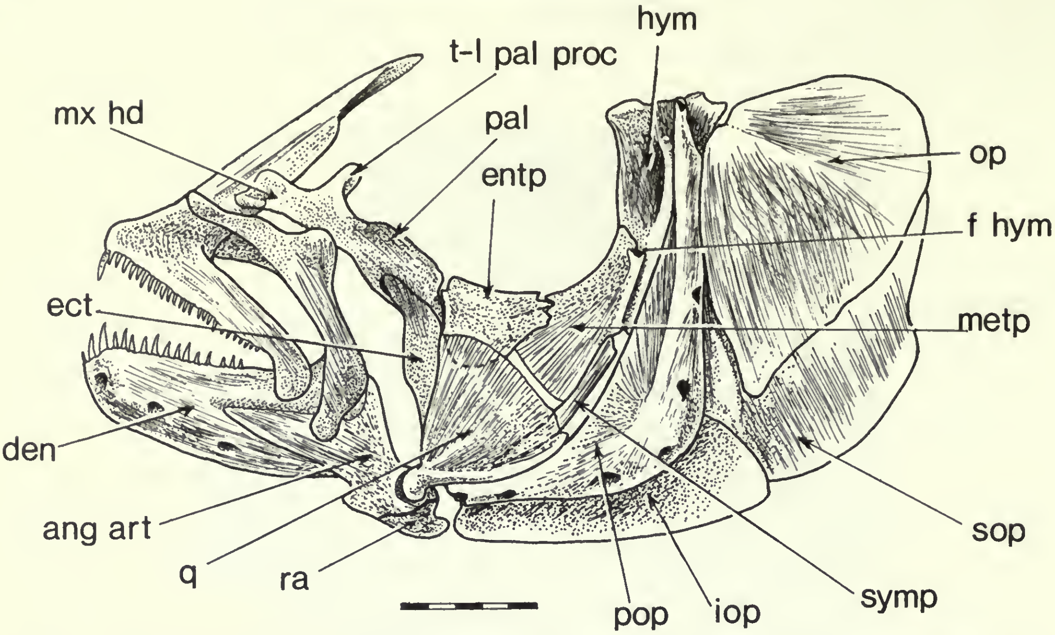


Fig. 6 *Hemichromis fasciatus.* Suspensorium, jaw elements and opercular series of the left side, in lateral view. The rostral cartilage has been removed (1976.11.12:135–7).

there is a stout, thumb-like, dorsally directed projection sloping backwards at a slight angle (Figs 3 & 7); it is this process which articulates with the compound facet on the anterior face of the lateral ethmoid (see p. 139). In frontal view the process is noticeably broadened over its distal half, and has a broadly rounded dorsal margin (Fig. 4). The posterior face and dorsal margin of this broadened region have the smooth appearance typical of articulatory surfaces. It is these areas which contact the facets of the lateral ethmoid. When the palatoquadrate arch is *in situ*, the rounded margin of the process lies just below the lower rim of the olfactory nerve foramen (Fig. 4). At the base of the process there is an ill-defined, low, anteromedially directed boss to which the palato-palatine ligament is attached (see p. 158).

The thumb-like process in *Hemichromis* is apparently the homologue of the low, transversely aligned mesethmoid process (*sensu* Barel *et al,* 1976) on the palatine of other cichlids.

The so-called lateral ethmoidad facet (Barel *et al,* 1976) which, in other cichlids, occupies the greater part of the palatine's dorsal margin posterior to the mesethmoidad process, is not developed in *Hemichromis*. Instead, this margin of the bone is produced into a low and thin flange delimiting an elongate depression on the medial face of the palatine (Fig. 21). This depression accommodates, in part, the palatine extension of the *adductor arcus palatini* muscle (see p. 156), and in part the head of the ectopterygoid.

On the palatine's medial face, very slightly behind the base of the thumb-like process, there is a stout and flat vomerine process (the palatine wing of Barel *et al,* 1976). The very clearly demarcated projection is directed ventromedially; its flattened posterior face articulates with the upper surface of the lateral process of the vomer (see p. 138).

For a short distance behind the origin of the vomerine process the ventral margin of the palatine is slightly excavated, the excavated part having a gently rounded margin which lies over the somewhat convex posterior face of the lateral process on the vomer (see p. 138).

The palatine in *H. bimaculatus* is more slender and far less robust than is the palatine of *H. fasciatus*. Otherwise, however, the bones in the two species show all the same characteristic features, except that the triangular prominence is very low and barely differentiated in *H. bimaculatus*.

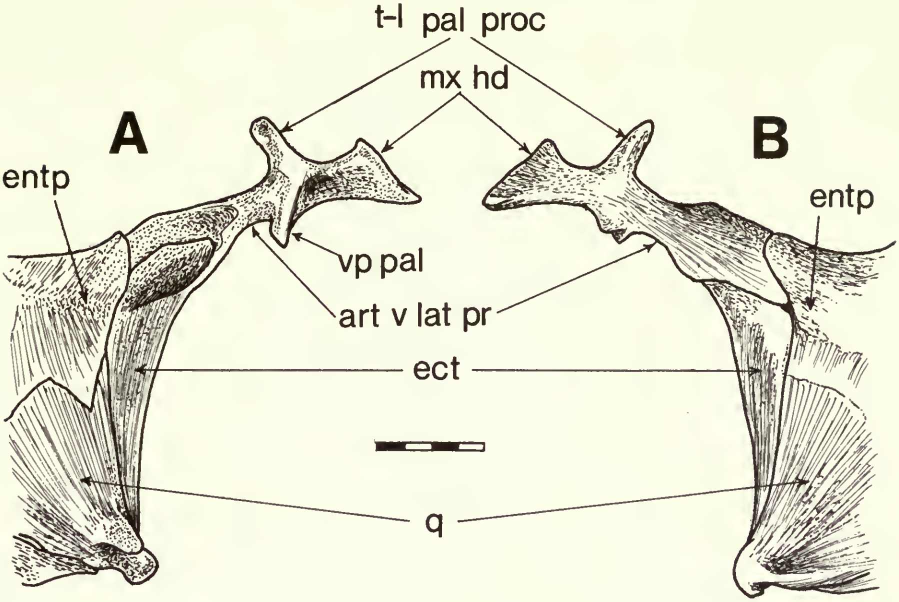


Fig. 7 *Hemichromis fasciatus*. Palatine and ectopterygoid, with entopterygoid in part. A. Medial aspect. B. Lateral aspect. (1953.4.28:243–4).

Posterodorsally, the *metapterygoid* in both species is in intimate contact with the ventral margin of the anterior flange of the hyomandibula, but no interdigitating suture is developed between the two bones (Fig. 6).

In the great majority of African cichlids examined (including *Pelmatochromis* and *Chromidotilapia*) as well as in several Neotropical taxa, the metapterygoid and the hyomandibular flange are not in contact or even closely apposed to one another. In some Neotropical species (eg *Cichla*) however, there is an extensive interdigitating suture between the bones (see Fig. 8). Unfortunately, much of the dry skeletal material of Neotropical species available to me is damaged in this part of the palatoquadrate arch, making it difficult to assess the modal condition in these fishes.

Amongst the so-called etropline cichlids (see Cichocki, 1976) which I could examine (*Etroplus suratensis* and *E. maculatus* [both Asian species], and *Paratilapia polleni, Ptychochromis oligacanthus* and *Paretroplus polyactis* [all Madagascan]), there is an intimate appositional or sutural contact between the metapterygoid and the hyomandibula's anterior flange. However, Van Couvering (1982: fig. 7c) illustrates a specimen of *Etroplus maculatus* (BMNH:659) in which there is no contact between these parts of the bones. Regrettably, this specimen is now extensively damaged and so it cannot be checked against Van Couvering's figure. In an alizarin preparation of this species, made from a specimen *ca* 33 mm standard length (BMNH 1889.2.1:3877–3881) the posterodorsal margin of the metapterygoid closely approaches the anterior flange of the hyomandibula, but does not contact it, thus resembling the situation figured by Van Couvering. In sharp contrast there is a distinct, albeit short, sutural union between the bones in a larger specimen, *ca* 50 mm standard length (alizarin prep., BMNH 1958.6.10: 68–74). These specimens would suggest, therefore, that the nature of the contact, or the lack of contact, is related to the fish's size. Thus it is important to note that all the other etropline material I examined (see above) was from specimens much larger than 50 mm standard length.

Judging from the outgroup taxa examined, and from descriptions in the literature, sutural contact between the anterior flange of the hyomandibula and the metapterygoid, or merely direct contact between them, is the plesiomorphic state (Johnson, 1980; see also Van Couvering, 1982).

In *Hemichromis* no *calyx* (see Barel *et al*, 1976:199; fig. 14A; also Fig. 8) is developed between

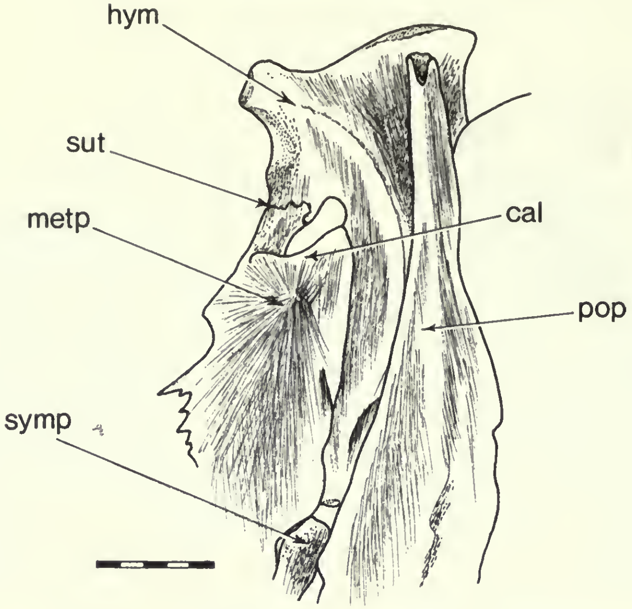


Fig. 8 *Cichla ocellaris.* Left metapterygoid and hyomandibula, in lateral view, to show the bones' sutural union, and the calyx (1895.3.29:30).

the metapterygoid and the hyomandibula. The majority of African taxa (including *Pelmatochromis, Pelvicachromis* and *Chromidotilapia*) have a well-developed calyx of the type described by Barel *et al (op. cit., loc. cit.)* in *Astatotilapia elegans.* In some species, however, the calyx's medioposterior wall, otherwise formed from either or both the metapterygoid and, or, the hyomandibular shank, is very poorly developed. Thus, in these species the calyx has only an anterior wall, derived from a circumscribed, anterolateral outpocketing on the posterodorsal face of the metapterygoid.

The calyx is absent in some Neotropical species (eg *Petenia splendida*), greatly reduced in others, and is present in either its completely or incompletely backed state (eg *Cichla*) in yet others. Its dorsal opening also shows a continuous size gradient, from small to expansive.

In all the etroplines examined (see above) a calyx is present and open-backed like that in *Cichla* (Fig. 8), and its dorsal opening ranges from small to large.

The presence of a calyx or calyx-like structure would seem to be a plesiomorphic feature amongst percoids (see Johnson, 1980; pers.observations). Its loss in certain cichlid taxa, including *Hemichromis,* could thus be interpreted as a derived condition. The distribution pattern of this apomorphy within the Cichlidae, however, renders it likely that the calyx has been lost independently on several occasions within Neotropical lineages of the family but, apparently, only once in Africa, namely in *Hemichromis.* Developmentally a calyx could be associated with a shift in the insertion of the *levator arcus palatini* muscle, which thereby prevents the formation of close contact between the anterior flange of the hyomandibula and the greater part of the metapterygoid's posterodorsal border.

Hyomandibula. The anterior flange is well-developed in both *H. fasciatus* and *H. bimaculatus* (Fig. 6). The shank of the bone is about two-thirds as long as the distance between the surface of the two articular heads and a line drawn horizontally through the ventral margin of the anterior flange.

Other elements of the suspensorium are illustrated in Fig. 6 and require no further comment except to note that there is no palato-entopterygoid gap, and that in the largest skeleton of *H. fasciatus* examined the posterior margin of the palatine is excavated to receive the anterior tip of the entopterygoid; in smaller specimens the two bones are merely apposed to one another (Fig. 21).

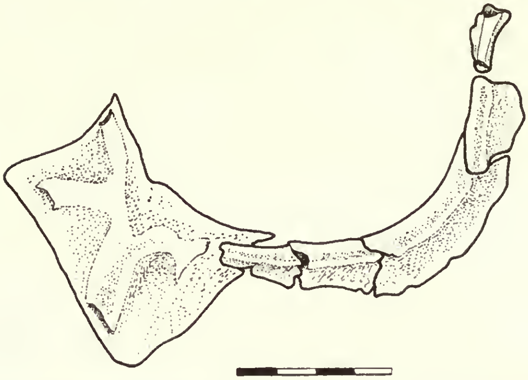


Fig. 9 *Hemichromis fasciatus*. Infraorbital bones, left side, in lateral view (1976.11.12:135–7).

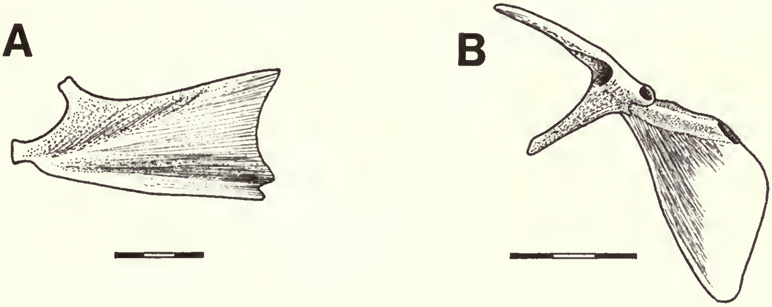


Fig. 10 *Hemichromis fasciatus*. A. Urohyal, in left lateral view. B. Left supracleithrum and posttemporal bones in articulation; lateral view (1976.11.12:135–7).

INFRAORBITAL BONES (Fig. 9)

These bones in *H. fasciatus* are illustrated in Fig. 9. According to Vandewalle (1971) there are, excluding the lachrymal (1st infraorbital) and dermosphenotic, only three bones in this series. However, the elongate 'third' element shown in his figure is, in fact, two bones, the upper of which is the shorter.

Laterally, the second infraorbital canal overlaps the posterior margin of the lachrymal. There is some interspecific variability in the extent of this overlap. *Hemichromis fasciatus* has only the tubular part of the second infraorbital continued forward, but in *H. bimaculatus* the flange of bone underlying the canal also extends onto the lachrymal. In all other respects the infraorbital series in the two species are similar.

POSTTEMPORAL AND SUPRACLEITHRUM (Fig. 10B)

Van Couvering (1982:20 & 22; fig. 10) recognised two types of *supracleithrum* in the cichlids she studied. In the supposedly plesiomorphic etropline type (which includes the tilapiine species examined by Van Couvering) the posterior opening for the lateral-line tubule is situated near the dorsal tip of the bone. In the supposedly derived haplochromine type the opening lies much further down, generally at a level slightly above the midpoint of the bone's posterior margin. Using that classification, *Hemichromis* has a haplochromine type of supracleithrum. The validity of Van Couvering's postulated polarity ratings for this feature remain to be tested on a much larger assemblage of species.

There are no obviously outstanding features in the morphology of the *posttemporal* (Fig. 10B). However, this element is rarely used in cichlid systematics and hence is not often illustrated or described.

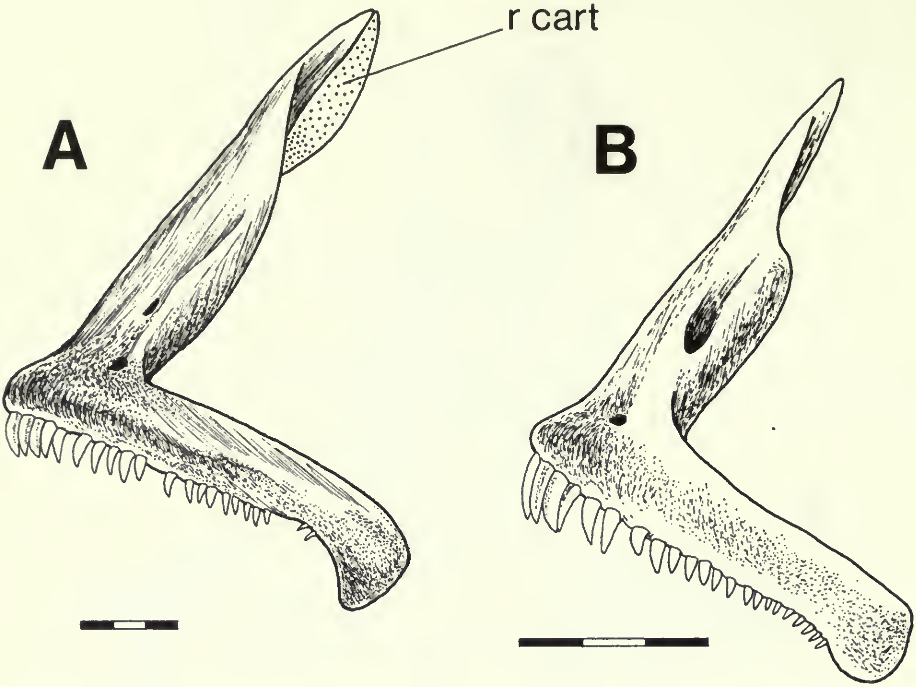


Fig. 11 A. *Hemichromis fasciatus*: premaxilla and rostral cartilage; left lateral view (1953.4.28:243–4). B. *H. bimaculatus:* premaxilla in left lateral view; rostral cartilage removed (unregistered specimen).

JAWS (Figs 6, 11, 12, 21)

The dentigerous arm of the *premaxilla* in *H. fasciatus* (Fig. 11A) is sharply and characteristically decurved posteriorly, with the result that its tip lies well below the level of the dentigerous area. The articular process extends distally along the lateral aspect of the ascending process almost to its tip; distally, the posterior margin of the articular process curves forward to become continuous with the anterior face of the ascending process. The rostral cartilage (Fig. 11A) is a relatively flat body, oval in outline, and with a maximum breadth only slightly exceeding those parts of the ascending process behind which it lies.

In *Hemichromis bimaculatus* (Fig. 11B) the posterior tip of the dentigerous arm is much less decurved, and the distal part of the articular process is more discrete than that in *H. fasciatus* (*cf* Figs 11A & B).

Both species have the length of the ascending process slightly less than the length of the dentigerous arm.

The other *Hemichromis* species show some variation in the degree to which the posterior tip of the premaxilla is decurved. In *H. frempongi, H. paynei* and *H. elongatus* the curvature equals that in *H. fasciatus*, but the condition in the remaining species is close to or identical with that in *H. bimaculatus*.

Maxilla (Fig. 12). Regan (1922) used the shape of the maxilla ('... maxillary narrow, curved') as one of two diagnostic features distinguishing *Hemichromis* from *Haplochromis*, the latter genus then containing the majority of fluviatile and lacustrine species in which the pharyngeal apophysis is of the *Haplochromis* type (see Greenwood, 1979). The maxilla in *Hemichromis* certainly does have a distinctive curvature (Fig. 12B) but in that feature it is approached, and equalled, by certain haplochromine species from Lake Victoria, although not by any of the generalized fluviatile species formerly identified as *Haplochromis* (see Greenwood, 1979). It was

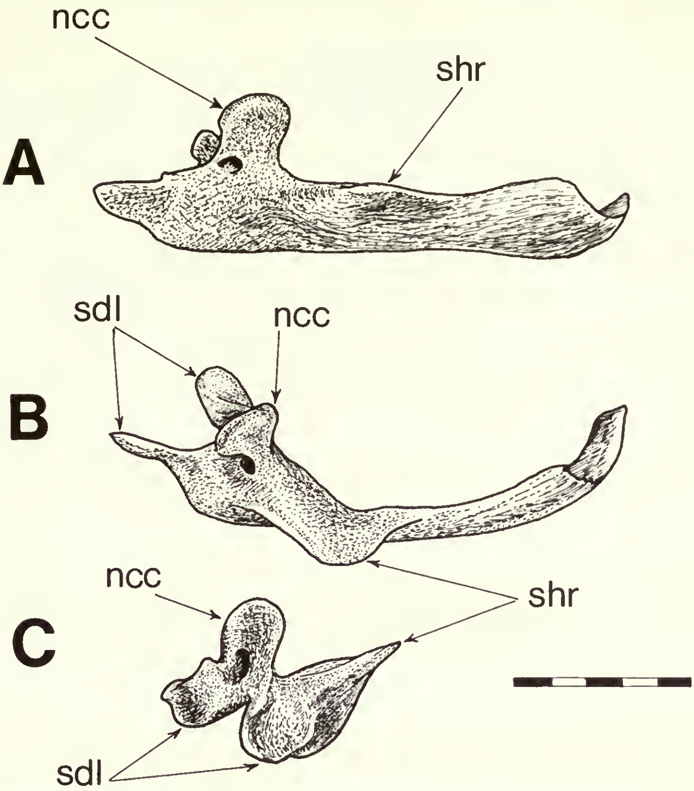


Fig. 12 *Hemichromis fasciatus*. Left maxilla in: A. Lateral, B. Dorsal, and C. Anterior views (1953.4.28:243–4).

these latter species with which Regan (1922) was presumably making his comparison since his paper was concerned with African and Syrian genera not restricted to the Great Lakes.

In dorsal view, the posterior part of the maxillary outline in *Hemichromis fasciatus* is a little more curved than it is in *Astatotilapia desfontainesi* (formerly a *Haplochromis;* Greenwood, 1979) and other generalized haplochromines. Anteriorly, however, the bone's mediad curvature is slightly less than in *A. desfontainesi* with the lateral arms of its premaxillary saddle lying in almost the same line as the anterior part of the shank (Fig. 12B).

When viewed laterally, the *Hemichromis* maxilla is relatively shallow, and the shank ridge is inclined outwards at a marked angle (Fig. 12A & C), both features distinguishing it from the maxilla in other African taxa.

The maxilla in *H. bimaculatus* has a more marked medial curvature than it does in *H. fasciatus,* is deeper, and its shank ridge inclines outwards at less of an angle. Also, in the former species the two arms of the premaxillary saddle are almost equal, whereas in *H. fasciatus* the lateral arm is noticeably longer.

Dentary (Fig. 6). In both *H. fasciatus* and *H. bimaculatus* the dentary is relatively short and moderately deep. It lacks a mental prominence in the symphysial region with the result that the chin is gently rounded and slopes posteroventrally. The ascending coronoid arm is slender in *H. fasciatus* but is wider in *H. bimaculatus.*

Both species have four external openings to the mandibular laterosensory canal, an unusual feature in cichlids where, as far as I can determine, the usual number is five. There are, however, only four, and in some species three, openings in *Etroplus*. The phyletic significance of mandibular pore numbers is uncertain. Amongst lower perciforms there are four or five, and in the labroids (excluding cichlids) three or four.

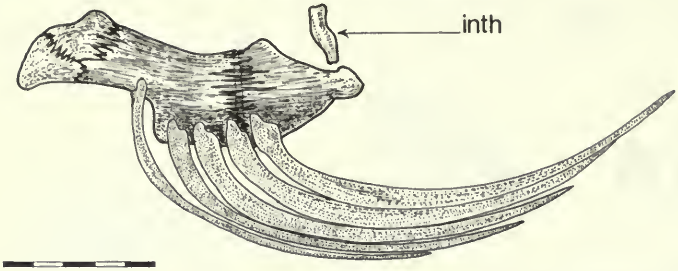


Fig. 13 *Hemichromis fasciatus.* Lower elements of left hyoid arch (excluding the basihyal), and branchiostegal rays; lateral view. (1976.11.12:135–137).

The posterior face of the vertical arm of the anguloarticular is expanded laterally, forming a distinct ledge onto which the *adductor mandibulae* 2 muscle inserts. The ledge in *H. bimaculatus* is relatively broader than that in *H. fasciatus,* and is distinctly concave (see comments in Stiassny, 1981*a*: 82–83, and Greenwood, 1983: 261).

An outstanding feature is the absence of a tunnel through the anguloarticular for the passage of the mandibulo-preopercular laterosensory canal in the ten species which could be thoroughly checked. Any connecting tubule between the laterosensory canals of the dentary and the preoperculum presumably must lie in the soft tissues of the region, but this could not be confirmed, with certainty, by dissection.

The absence of a laterosensory canal in the anguloarticular is a most unusual feature, one which has not been described in any other cichlids, and which with one exception (see p. 168) was not found in any of the numerous osteological preparations I examined.

HYOID ARCH AND UROHYAL (Figs 6, 13 & 10A)

Little has been published on the hyoid arch in cichlid fishes (Vandewalle, 1971; Goedel, 1974, Barel *et al,* 1976) and since I did not study these elements in taxa other than *Hemichromis,* few comparative statements can be made.

The hyoid arch (Fig. 13) seems to differ but slightly from that in *Astatotilapia elegans,* described in detail by Barel *et al* (1976), although in *Hemichromis* there is relatively less distance between the articulatory points for the first and second branchiostegal rays.

The morphology of the *urohyal* in cichlids has also been little studied (see Stiassny, 1981*a*:98). This bone in *Hemichromis fasciatus* (Fig. 10A) is somewhat elongate, with a prominent, anteriorly directed spine, and well-defined ventral wings enclosing a deep ventral wing fossa (terminology that of Barel *et al,* 1976). Dorsally, the base of the spine is continued backwards as a low ridge extending over about two-thirds of the bone's posterior length. The ridge runs the entire length of the dorsal ridge-groove but is displaced dextrally so that the right side of the groove is much smaller than the left, persisting merely as a ledge along the spine's posteriorly attentuated base. In those respects the urohyal of *Hemichromis fasciatus* differs quite markedly from that in *Astatotilapia elegans* (see Barel *et al* 1976:237, fig. 40).

DORSAL GILL-ARCH SKELETON (Figs 14B, 15 & 16)

The overall morphology and arrangement of these elements closely approach those of *Astatotilapia calliptera* and *A. elegans* (see Stianssy, 1981*b*, fig. 6 and Barel *et al,* 1976), a pattern which can be taken to represent the modal African cichlid condition.

As in *Astatotilapia,* pharyngobranchial 2 lies at right angles to the long axis of pharyngobranchial 3, and is directed transversely across its anterior border. Pharyngobranchial 3 differs slightly from that element in *Astatotilapia* because of its more nearly square outline. As in *Astatotilapia* it is intimately associated with upper pharyngeal tooth plate 4.

All four epibranchials, but particularly those of arches 1 and 2, are relatively more elongate than their counterparts in *Astatotilapia,* but are not as elongate as those in *Cichla* (see Stiassny, 1982: 431, fig. 2).

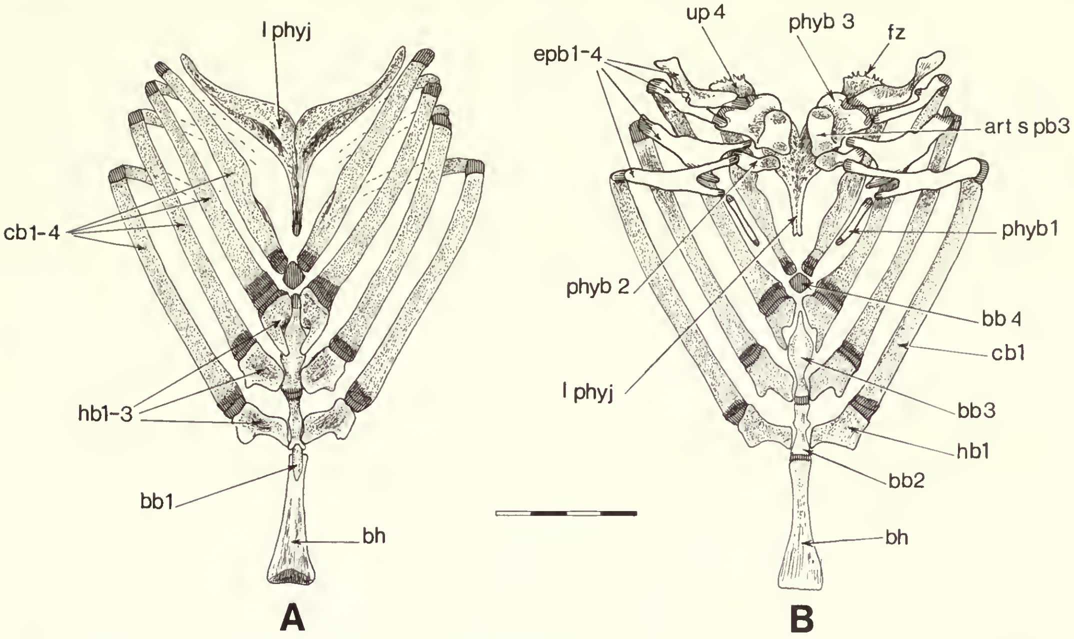


Fig. 14 *Hemichromis fasciatus.* Gill-arch skeleton in: A. Ventral, and B. Dorsal views (1976.11.12:135–7; alizarin-alcian blue transparency).

The angle formed between the two arms of epibranchial 1 is about 25°; the posterior arm is almost twice the length of the anterior one and is directed caudad relative to the major axis of the bone. In the two latter characters, epibranchial 1 exhibits what seems to be the typically 'African' condition for the bone, but the angle between the arms is less than in other African species and thus approaches the condition usual in Neotropical taxa (Cichocki, 1976:84, fig. 1.16). My observations on the condition of epibranchial 1 in *Hemichromis fasciatus* differ somewhat from those of Cichocki who, unfortunately, gave no illustration of the bone in this species. According to Cichocki (1976:84), the two arms make an angle of 35° or more, and the posterior arm is directed strongly caudad.

The full significance of these various characters is difficult to assess because so little information is available from African taxa. Cichocki (1976:84) has, however, provided many data for the Neotropical species, and also discusses their possible phylogenetic significance.

As in *Astatotilapia,* and many other African taxa, but unlike *Cichla* and many Neotropical taxa (see Stiassny, 1981:295), there is no interarcual cartilage in *Hemichromis.*

Epibranchial 2 differs from that in *Astatotilapia,* and most other cichlids in which the feature has been checked, in having a very greatly reduced cartilaginous extension to its anterior border (Stiassny, 1981*a* & *b*, 1982; Barel *et al,* 1976; Trewavas, 1973; personal observations). In *Hemichromis* only the protracted tip of the cartilage is visible as a projection below the anterior margin of epibranchial 1. The cartilage is reduced, and probably more so, in *Cichla* (see Stiassny, 1982: 431, fig. 2) and in *Orthochromis machadoi,* an African species (Greenwood, 1984: 210).

Epibranchial 4 articulates with pharyngobranchial 3, but has a strong ligamentous connection with the head of the 4th upper pharyngeal tooth plate as well (see Stiassny, 1981*b*:293, footnote, for use of the term 4th tooth plate). A prominent 'frayed zone' is associated with the posterior margin of the tooth-plate.

The quadrangular region (*sensu* Barel *et al,* 1976) of epibranchial 4 has a more elongate outline and is less expansive in *Hemichromis* than in most African cichlids examined (see Figs 15 & 16) or those illustrated elsewhere (Barel *et al,* 1976; Stiassny, 1981*a* & *b*, 1982). It would thus appear to

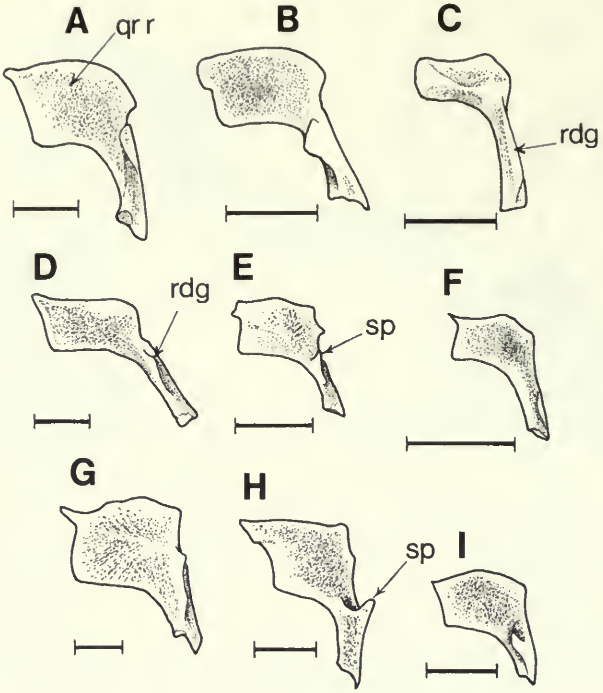


Fig. 15 Fourth epibranchial bone (right), in posterior view, of various cichlids to show outline of quadrangular area and variation in the development of the shank spine or ridge. A. *Astatotilapia macropsoides* (unreg. specimen). B. *Chromidotilapia kingsleyae* (1934.8.31:179–188). C. *Cichla ocellaris* (1973.3.26:1–6). D. *Hemichromis fasciatus* (1976.11.12:135–7). E. *Chromidotilapia finleyi* (1973.5.4:63–7). F. *Aequidens portalagrensis* (1972.10.17:3538–51). G. *Ptychochromis oligacanthus* (1882.2.25:173). H. *Oreochromis niloticus* (1960.9.30:158–72). I. *Trematocara unimaculatum* (1961.11.22:519–525).

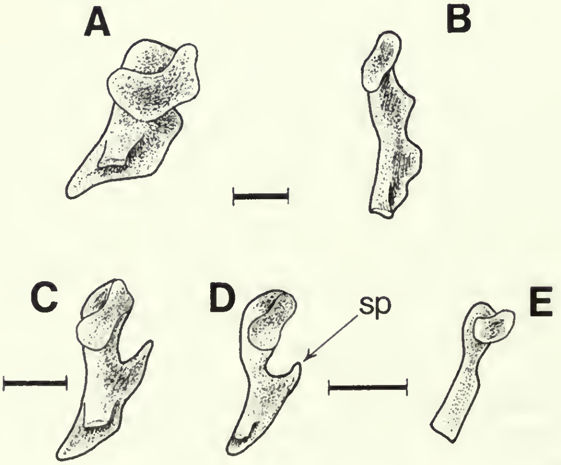


Fig. 16 Fourth epibranchial (right) in medial view to show variation in development of the shank spine or ridge in: A. *Ptychochromis oligacanthus*. B. *Hemichromis fasciatus*. C. *Astatotilapia macropsoides*. D. *Chromidotilapia kingsleyae*. E. *Cichla ocellaris*.

represent the pleisomorphic state for this character (personal observations and comments in Stiassny, 1981*b*). The shank spine on epibranchial 4 is little more than a low ridge, albeit a well demarcated one (Figs 15 & 16). In this respect it is intermediate between the condition seen in Neotropical taxa and that in the Madagascan etropline *Ptychochromis* where the ridge, although shorter is somewhat more elevated; the ridge in the Neotropical species is very low and long.

Judging from the condition of the shank spine (or ridge) in serranids, centropomids and non-cichlid labroids, a well demarcated spine is the derived condition. Amongst African cichlids, the type of ridge found in *Hemichromis* must therefore be considered plesiomorphic.

Ventral gill-arch skeleton (Fig. 14A)

Loiselle (1979) describes and illustrates the lower pharyngeal bones and dentition in all the *Hemichromis* species recognized by him. Apart from the lower pharyngeal bone, ventral gill-arch elements have been little used in cichlid systematics. That fact, combined with the very unsatisfactory condition of the gill arches in most skeletal preparations available to me, preclude any detailed comments on these bones in *Hemichromis*.

Microbranchiospines

According to Loiselle (1979:11), microbranchiospines are not present in any species of *Hemichromis,* a statement which is completely contradicted by my observations. These show that microbranchiospines are present on the outer aspect of gill arches 2 to 4 in *H. fasciatus, H. bimaculatus, H. letourneauxi, H. cerasogaster, H. guttatus, H. frempongi* and *H. paynei*; suitable material of the other species was not available.

In at least some individuals of *H. fasciatus,* microbranchiospines are present on both faces of certain arches. An alizarin preparation, *ca* 80 mm standard length (BMNH 1976.11.12:135–7), has these structures on the outer face of arch 2, on both faces of arch 3 (but probably restricted to the lower part of the inner face), and on both faces of arch 4 (again probably with a restricted distribution, in this instance to the upper regions).

A double-sided distribution was not found in other *H. fasciatus* specimens (both stained and unstained, in the size range 60–120 mm SL), nor was it found in any other species of the genus. Interestingly, Stiassny (1981*b*:304) records microbranchiospines on both sides of arches 1–4 in *Cichla* and *Etroplus*. To the best of my knowledge there are no records of other cichlid species showing a similar distribution pattern.

Caudal skeleton (Fig. 17)

Those specimens of *H. fasciatus* which I examined differ in no appreciable way from that illustrated by Vandewalle (1973:fig. 1). That figure does not, however, indicate the cartilages associated with the fin skeleton, some of which are shown in Fig. 17 below. Although not represented in that figure, cartilage is also present along the posterior margin of the epurals, hypurals, pharhypural and the haemal spine on the second preural vertebra. Because the cartilage has stained irregularly in the specimens I examined it is impossible to tell whether, as in *Cichla*, it is in the form of two bands continuous with, respectively, the dorsal and ventral accessory cartilage masses (see Fig. 17). Certainly there is no trace of a cartilage plate between and connecting hypurals 2 and 3, a feature which Stiassny (1982:450) considers an apomorphy of *Cichla*.

In two alizarin-alcian blue stained specimens of *H. bimaculatus* the caudal skeleton differs from that in *H. fasciatus* in having no hypurapophysis on the parhypural, and in having a less expansive neural arch and spine on the second preural centrum.

Both *H. fasciatus* and *H. bimaculatus* have I+7, 7+I principal caudal rays, together with a number of much shorter rays preceding them.

No fused hypurals were found in the specimens of *H. fasciatus* examined, although hypurals 1 and 2, and 3 and 4 are very closely apposed. In one *H. bimaculatus* none of the hypurals is closely apposed, but in other specimens hypurals 3 and 4 are closely applied to one another along their entire lengths.

From what is known about the caudal fin skeleton in cichlid fishes it does not seem likely that it will prove to be of use in determining intrafamilial relationship (see also Vandewalle, 1973).

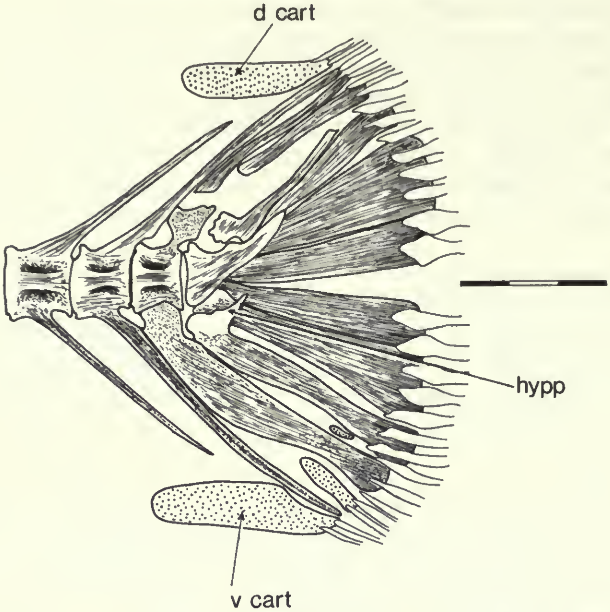


Fig. 17 *Hemichromis fasciatus*. Caudal fin skeleton; only the larger cartilages are illustrated. (1976.11.12:135–7).

PECTORAL GIRDLE (Fig. 18)
The pectoral girdle apparently provides few characters of value for establishing phylogenetic relationships amongst the cichlids (see Cichocki, 1976; Stiassny, 1982).

Both these authors note the presence in the Neotropical genera *Cichla* and *Crenicichla* of a prominent, anterodorsally directed spine on the head of the second postcleithrum, and Stiassny (1982:448) records a small process, similarly directed, on the head of that element in three other Neotropical genera, *Petenia, Acaronia* and, in some species, *Cichlasoma*. In *Cichla* and *Crenicichla* the process is associated with a sheet of muscle extending from the first pleural rib, but in the other species the process does not serve as a site for muscle attachment (Stiassny, 1982:448).

A small and short, but obvious process is present on the second postcleithrum in *Hemichromis* (Fig. 18B); it is less well differentiated than the process in *Petenia,* and, as in that species, it does not seem to be associated with a muscle sheet from the first rib. The presence of this short process gives the head of the second postcleithrum a more rectangular and broader outline than that present in other African and in Neotropical species.

Stiassny (1982:448) discusses the phyletic significance of the postcleithral process, especially in relation to its presence in *Cichla, Crenicichla* and the serranid genus *Serranus*. She favours homoplasy as an explanation of these interfamilial occurrences. The reduced (or poorly developed) spine in *Hemichromis* and in certain Neotropical taxa is probably open to the same interpretation.

VERTEBRAL COLUMN
An apophysis for the origin of the *retractor arcuum branchialis* muscles, Trewavas' (1982:9) spondylophysial apophysis, is developed on the third abdominal vertebra in *H. fasciatus* and *H. bimaculatus*; its presence could not be checked in the radiographs of the other species.

Epipleural ribs are present on all but the last 3 or 4 pairs of pleural ribs in both species, and epicentral ribs occur on the first two centra (which do not carry pleural ribs).

None of these features could be determined with certainty (or even at all) from the radiographs

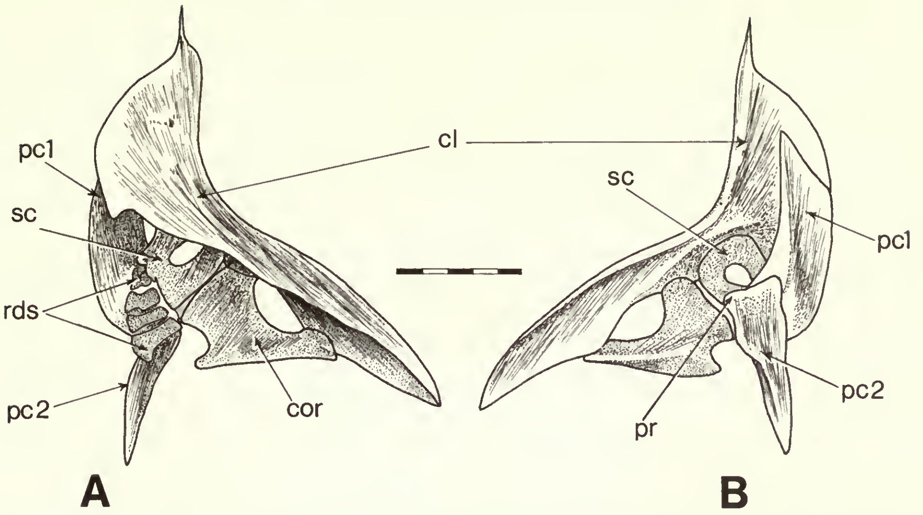


Fig. 18 *Hemichromis fasciatus*. Pectoral girdle in: A. Lateral view, B. Medial view (1976.11.12:135–7).

of the other *Hemichromis* species. *Vertebral counts* were made, and are listed below. It would seem from those figures that two intrageneric groups can be recognised, one with a higher total count (*ie* 26–28, mode 27) than the other (25, less frequently 26). The higher count is attributable to an increase in the number of abdominal centra.

In the list below, frequencies are indicated by f, and modes are in bold type. The fused PU_1 and U_1 centra are excluded from all counts.

Group I:	
H. fasciatus:	27 or **28**, comprising **15** abdominal + 12 (f5) or **13** (f7) caudal centra
H. elongatus:	26 or **27**, comprising 14 (f1) or **15** (f11) + **12**(f12)
H. frempongi:	**27** (f13) or 28 (f2), comprising 14 (f1) or **15** (f14) + **12** (f12) or 13 (f3)
Group II:	
H. bimaculatus:	**25** (f7) or 26 (f1), comprising **13** (f6) or 14 (f2) + 11 (f1) or **12** (f7)
H. cristatus:	25 comprising 12 + 13 (Holotype: 1969.3.26:76)
H. paynei:	**25** (f17), comprising **13** (f17) + **12** (f17)
H. guttatus:	**25** (f2), comprising **13** (f2) + **12** (f2)
H. stellifer:	**25** (f3) comprising **13** (f2) or 14 (f1) + 11(f) or **12** (f2) (Paratypes AMNH 16864)
H. cerasogaster:	**25** (f4) comprising **13** (f4) + **12** (f4)
H. letourneauxi:	**25** (f15) or 26 (f5), comprising 12 (f2) or **13** (f18) + **12** (f14), 13 (f5) or 14 (f1)
H. lifalili:	**25** (f5) comprising **13** (f5) + **12** (f5)

Myology

JAW MUSCLES (Figs 19–21)

As Vandewalle (1971:271; fig. 6) noted in his description of *H. fasciatus*, these muscles are well-developed. *Adductores mandibulae* 1 and 2 are bulky, with *Adductor* 2, at its midpoint, about two and three quarters times deeper than *Adductor* 1 (Fig. 19). *Adductor* 3 is also a large muscle, the lower part of which exchanges fibres with *Adductor* 2; it inserts on the coronomeckelian ossification.

The A_w division of the adductor complex covers about two-fifths of the inner aspect of the lower jaw (Fig. 21). As compared with the condition of this muscle in those cichlids in which it has been described (Anker, 1978; Stiassny, 1981*a* & *b*, 1982), the central aponeurosis is reduced and, consequently, the muscle is more musculose; its fibres, particularly those on the lower half of the muscle, are arranged almost horizontally. Posteriorly A_w has a tendinous attachment to the medial face of the quadrate (Fig. 21). At that point the tendon is narrow, and remains narrow as it passes across the quadrato-mandibular joint.

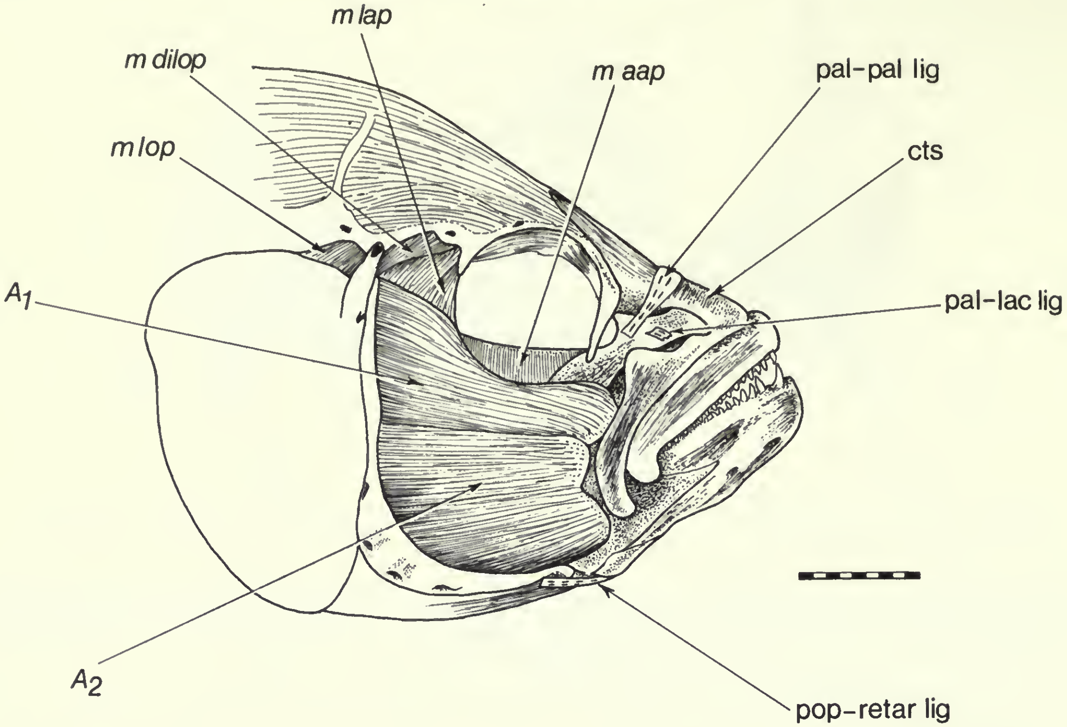


Fig. 19 *Hemichromis fasciatus*. Superficial muscles of the jaw and suspensorium, and superficial jaw ligaments. Only the proximal end of the palatolachrymal ligament remains after removal of the lachrymal bone (1953.4.28:423–4; 115 mm SL).

Unlike the tendon A_1b described in other cichlids, the A_1b tendon in *Hemichromis fasciatus* first merges completely (and not just partially) with the tendon of A_w before, as a discrete entity again, it inserts on the nipple process of the anguloarticular (Fig. 21).

The origins and insertions of the adductor complex follow the usual cichlid pattern (see Anker, 1978; Stiassny, 1981*a* & *b*, 1982). The stout tendon of *Adductor* 1 has a long area of insertion ventrally on the anteromedial face of the maxilla, extending between the neurocranial condyle of that bone and a line drawn through the anterior margin of its shank ridge.

An *intermandibularis* muscle is present, and has no outstanding features.

The *levator arcus palatini* (Figs 18 & 19) is a bulky muscle, rhomboidal in outline. It originates on the sphenotic and inserts onto the hyomandibula and upper part of the metapterygoid. Its insertion is confined to the lateral, that is outer, aspects of these bones since no calyx is developed (see p. 145).

The *adductor arcus palatini* (Figs 19 & 20) is a thick, well-developed muscle, from which a small anterior portion extends forward onto the palatine, filling the recess in the posterior part of that bone (see p. 144) and the recess in the dorsal part of the ectopterygoid. No such extension of the muscle was noted or figured by Vandewalle (1971:271; fig. 5), but its presence in all specimens of *H. fasciatus* (and those examined by Cichocki [1976]) suggests that it must have been overlooked by that author.

A palatinad extension of the *adductor arcus palatini* is a characteristic of all the African cichlids I have examined and those studied by Cichocki (1976), although it is absent in *Heterochromis* (M. K. Oliver, pers. comm.). No extension was found in the many Neotropical cichlids examined by Cichocki, and it is also wanting in the etropline species, including those from Madagascar, which he examined (Cichocki, 1976: 201).

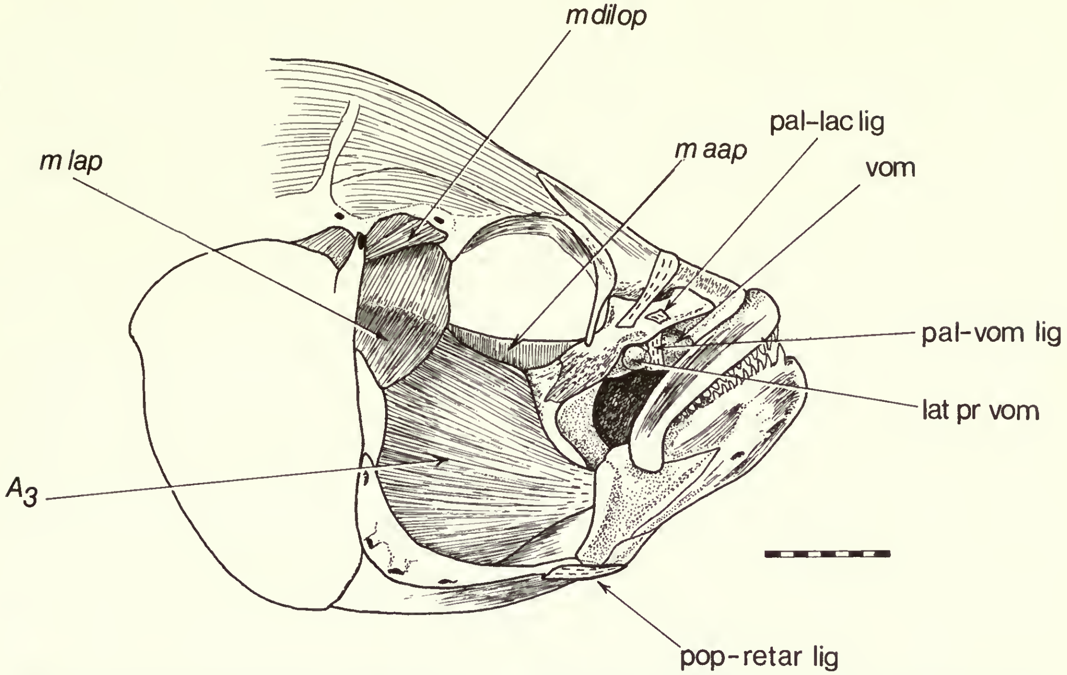
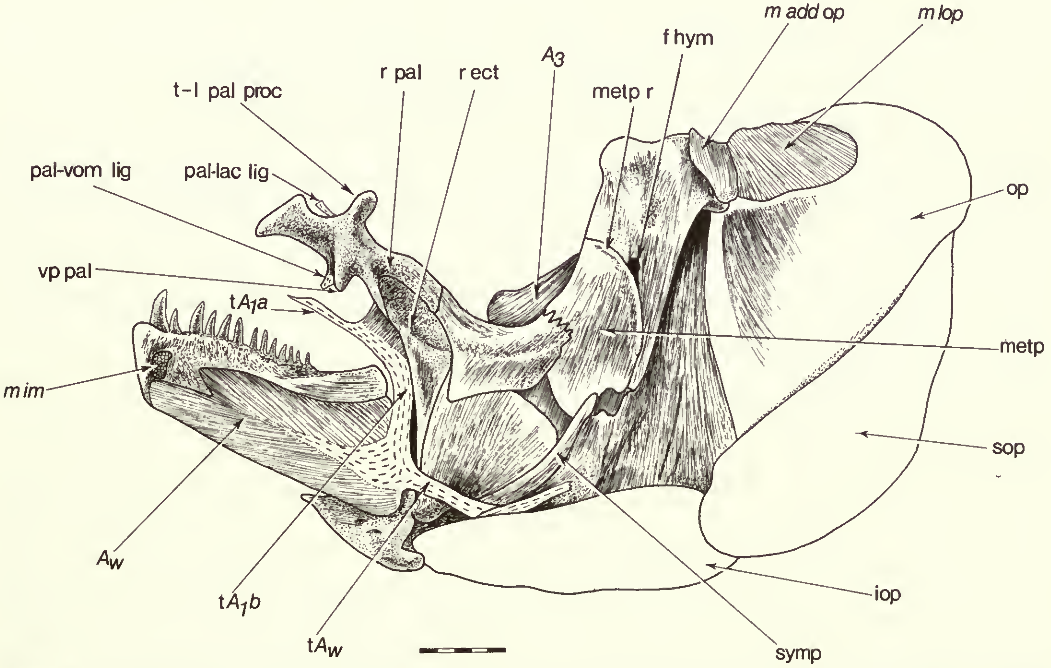

m dilop
pal-lac lig
m lap
m aap
vom
pal-vom lig
lat pr vom
A3
pop-retar lig

Fig. 20 *Hemichromis fasciatus*. Deeper jaw and suspensorium muscles. The maxilla has been removed to show, in part, the palatovomerine ligaments and also the lateral process of the vomer articulating with the palatine.


m add op
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A3
r pal
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metp r
t-l pal proc
pal-vom lig
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tA1a
metp
m im
sop
Aw
iop
tA1b
tAw
symp

Fig. 21 *Hemichromis fasciatus*. Medial view of right suspensorium and dentary to show the A_w muscle and its tendons, and the tendon system associated with *m. adductor mandibulae* 1. The articulatory processes of the palatine, and the recessed medial faces of the palatine and ectopterygoid (for the insertion of the extended *m. adductor arcus palatini*) are also visible.

LIGAMENTS ASSOCIATED WITH JAWS AND PALATOPTERYGOID ARCH IN *H. fasciatus* (Figs 19–22)

A broad swathe of very dense connective tissue extends across the ascending processes of the premaxillae, connecting the maxilla and palatine of each side, and those of opposite sides, with one another. Its points of origin are along the anterior margin of each maxilla (from the anterodorsal tip to the level of the facet for articulation with the palatine), and from the anterodorsal margin of the palatine, including the triangular prominence (see p. 143). Dorsally, this sheet is continuous with the lower margin of the palato-palatine ligament which, however, is readily distinguishable by its more densely compacted tissue, and hence its appearance.

The *palato-palatine* ligament itself originates on each palatine from a marked prominence below the ethmoid articulatory process of the bone. It broadens as it passes across the premaxillary ascending processes, where it appears to become continuous with the connective tissue sheet described above.

Anterior to, and a little below the level of the boss to which the palato-palatine ligament is attached, there is a shallow, elongate groove on the lateral face of the palatine. A broad-based ligament, the *palatolachrymal*, originates from this groove, and inserts on the lachrymal (1st infraorbital bone). Vandewalle (1971; fig. 5) illustrates a ligament in this position (labelled 1i3) which he identifies as the palato-maxillary ligament. There are, however, no palato-maxillary ligaments in this position in *H. fasciatus;* Vandewalle's 1i3 is, in fact, the proximal part of the palato-lachrymal ligament, its distal portion having been detached with the lachrymal bone during dissection (see Figs 19–21).

The absence of well-defined *palatomaxillary* ligaments in *Hemichromis* is a most noteworthy feature. In all other African cichlids examined a clearly defined ligamentous band passes over the palato-maxillary articulation, attaching the palatine head to the underlying lateral face of the maxilla (*ie* Cichocki's [1976:81] *anterodorsal palatomaxillary* ligament); in *Hemichromis* there is only a weak connective tissue linkage between the bones at this point, or at most a few clearly ligamentous strands of tissue. In the other African cichlids I examined there is a second and strong ligament which, originating from a discrete process below the spur for the palato-palatine ligament, inserts on the head of the maxilla immediately behind the anterodorsal palatomaxillary ligament. This ligament Cichocki (1976: 80–81) calls the *anteroventral palatomaxillary* ligament. It too is absent in *Hemichromis* (specimens of all species except *H. cristatus* were dissected).

Cichocki (1976:81) comments on the absence of an anteroventral palatomaxillary ligament in the Neotropical cichlids, and its presence in all the African species he examined and in others studied by Liem & Osse (1975), *ie Astatotilapia burtoni, Oreochromis niloticus, Tropheus moori* and *Eretmodus cyanostictus*. I can confirm its presence in all the African species I dissected (see p. 133), except, of course, *Hemichromis*. Another African species, *Pterochromis congicus* may also lack this ligament, but the material dissected was poorly preserved so its apparent absence in that species must be treated as unconfirmed.

An anteroventral palatomaxillary ligament is definitely present in the Madagascan and Asian etropline cichlids examined, *viz: Etroplus maculatus, Paretroplus dami, Paratilapia polleni* and *Ptychochromis oligacanthus* (see Cichocki, 1976; also pers. observations).

In all the eight *Hemichromis* species dissected (see p. 133) there are no vertically aligned *ethmopalatine ligaments* (Stiassny's [1981*a*] palatine lateral ethmoid ligament). This ligament, or ligaments since there may be two or even three contiguous divisions, is present in the majority of African taxa I examined, but it is absent in at least three species from Lake Tanganyika, *Bathybates, Hemibates* and *Trematocara* (see Stiassny, 1981:97; figs 13, 14 & 20). Fewer data are available on these ligaments in Neotropical species, but personal observations suggest that one or more is generally present.

It could be argued that the absence of lateral ligamentous connections between the ethmoid and palatine in *Hemichromis* is correlated with the unusual way in which the bony palato-ethmoidal joint has been effected in that genus (see p. 138). That argument cannot, however, be used to explain their absence in *Bathybates, Hemibates* and *Trematocara.* These species have the modal, and plesiomorphic, anterior palato-ethmoidal articulation found in other African cichlids, in many Neotropical taxa, and amongst lower percoids as well; see discussion on p. 166 below.

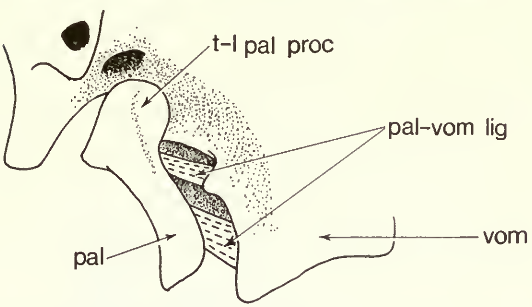

Fig. 22 *Hemicromis letourneauxi.* Semi-schematic sketch to show the typical *Hemichromis* type of palatovomerine ligament system; viewed from above and anterolaterally. The palatine bone has been dislocated from its articulation with the lateral ethmoid and moved a little outwards and downwards (1907.12.2:2969–84).

All the African and Neotropical cichlids I examined do have a posterior ethmo-palatine ligament, namely one between the posterior (*ie* intraorbital) face of the lateral ethmoid and the posterior wing of the palatine. In *Hemichromis* this ligament can be absent in one species, is thin and weakly developed in others, but is stout and well-developed in the majority. Vandewalle (1971:271, fig. 5) illustrates a posterior ligament in *Hemichromis fasciatus* and comments on its more posterior position in that species relative to *Tilapia guineensis.* However, Vandewalle appears to have confused the anterior palato-lateral ethmoid ligament in *T. guineensis* with the posterior and intraorbital ligament in *H. fasciatus.* The latter ligament is also present in *T. guineensis,* and occupies a position comparable with that in *H. fasciatus.*

At present little is known about the nature and occurrence pattern of palato-ethmoidal ligaments in percoids and especially in cichlids. Based on out-group comparisons with other percoids (eg Serranidae and Centropomidae) it seems that the presence of anterior palato-ethmoidal ligaments is a derived condition, but that a posterior (*ie* intraorbital) ligament is a primitive feature. Another 'primitive' ligament is that between the palatine and the mesethmoid; such a ligament is present in some cichlids (see Stiassny, 1981a:76) but is wanting in the majority, including *Hemichromis.*

Judging from the presence/absence pattern of lateral palato-ethmoid ligaments in cichlids, their absence might well be considered as a secondary loss (*ie* a derived condition), possibly one associated with the functional-structural characteristics of the bony palato-ethmoidal articulation. Until that possibility has been explored, both in cichlids and out-group taxa, little that is worthwhile can be said about their value as indicators of phyletic relationship.

There is a double *palatovomerine ligament* system in *Hemichromis* (Fig. 22). Ventrally, a strong ligament runs from the medial aspect of the palatine to insert on the ventrolateral face of the vomerine fossa, immediately in front of the lateral vomerine process on which the palatine articulates and is supported (see p. 138). Dorsally, a broad but less robust ligament connects the base of the thumb-like process on the palatine with the vomerine fossa; it inserts slightly above the ventral ligament.

DORSAL GILL-ARCH MUSCULATURE (Figs 23–25)

These muscles conform to what is apparently the typical cichlid pattern (see Anker, 1978; Stiassny, 1981*a* & *b*, 1982; Liem & Greenwood, 1981; Kaufman & Liem, 1982).

The *transversus dorsalis anterior* muscle, as in all cichlids, is tripartite, with the *musculus transversus pharyngobranchialis* 2 division marginally the smallest element, and the *m. craniopharyngobranchialis* 2 clearly the largest.

The *mm levatores externi* 1–3 are of approximately equal size. The fourth muscle is distinctly enlarged; the greater part inserts, through a short tendon, onto the horn of the lower pharyngeal bone (the fifth ceratobranchial). A small, lateral slip of this muscle inserts, tendinously, on the fourth epibranchial.

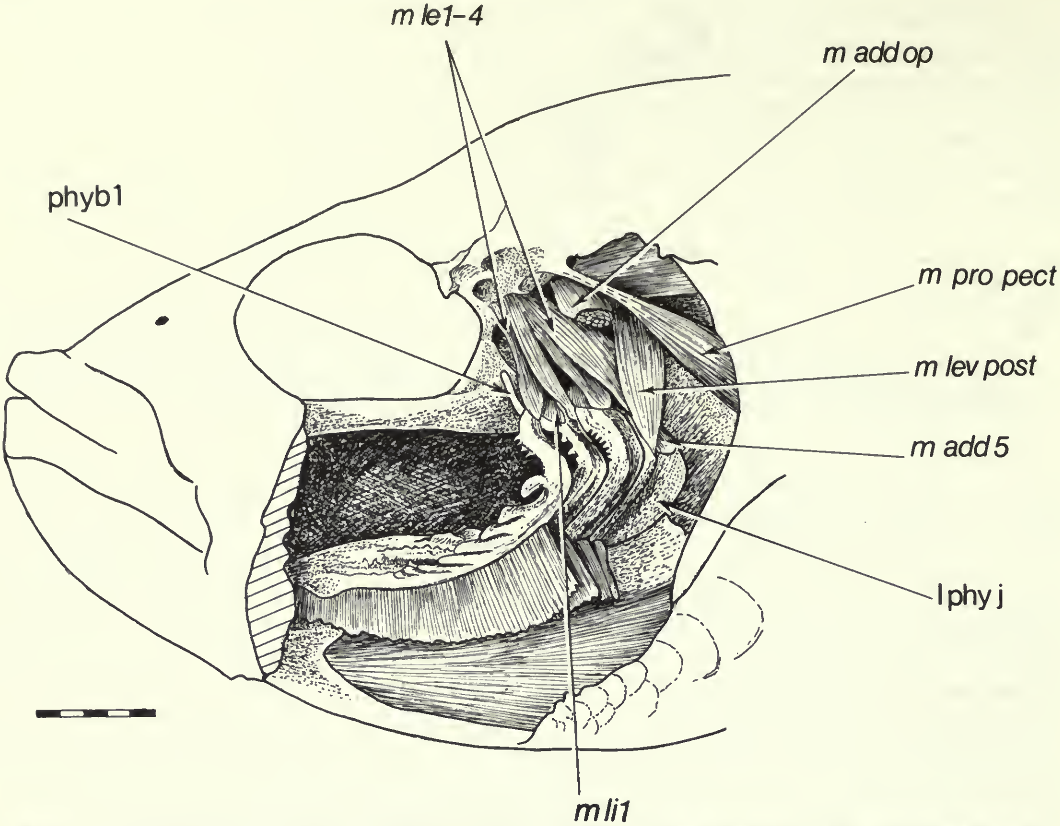

Fig. 23 *Hemichromis fasciatus.* Dissected head to show the superficial and lateral gill-arch musculature. Gill filaments have been removed from the upper parts of the gill-arches.

The two *mm levatores interni* are each of approximately the same bulk, with the second being very slightly the larger of the pair.

The *m. levator posterior* is well-developed, with a cross-sectional area about one third that of the *m. levator externus* 4. It inserts both on the fourth epibranchial, laterally, and on the horn of the lower pharyngeal bone medially. The greater part of its insertion, however, is on the epibranchial. Only a small slip is continuous with the underlying lateral division of the *m. obliquus dorsalis posterior* and thus comes to insert on the lower pharyngeal horn (see Aerts, 1984, whose terminology is followed here).

Based on the condition seen in certain other African cichlids I examined (eg *Aulonocranus dewindtii*) where there is greater continuity between the *m. levator posterior* and the lateral division of the *m. obliquus dorsalis posterior,* the situation in *Hemichromis fasciatus* must be considered plesiomorphic.

Hemichromis is not unique in this respect since it is paralleled in *Astatotilapia elegans* (see Anker, 1978), *Cichla ocellaris* (Stiassny, 1982; fig. 6; pers. obs.), and *Aequidens vittatus* (pers. obs.).

From the various published figures of the dorsal gill-arch musculature in cichlids, it would seem that the lateral division of the *m. obliquus dorsalis posterior* has either been overlooked or else treated as part of the fifth adductor muscle (which connects the fourth epibranchial with the horn of the lower pharyngeal bone). The role of the oblique posterior muscle in the evolution of cichlid pharyngeal jaw musculature was clearly demonstrated by Aerts (1982). A detailed study of increasing association between the oblique posterior and the posterior levator muscles in cichlids has yet to be made; it is this change which presumably underlies Kaufman & Liem's (1982) character 'Predisposition for insertion of levator posterior muscle on lower pharyngeal

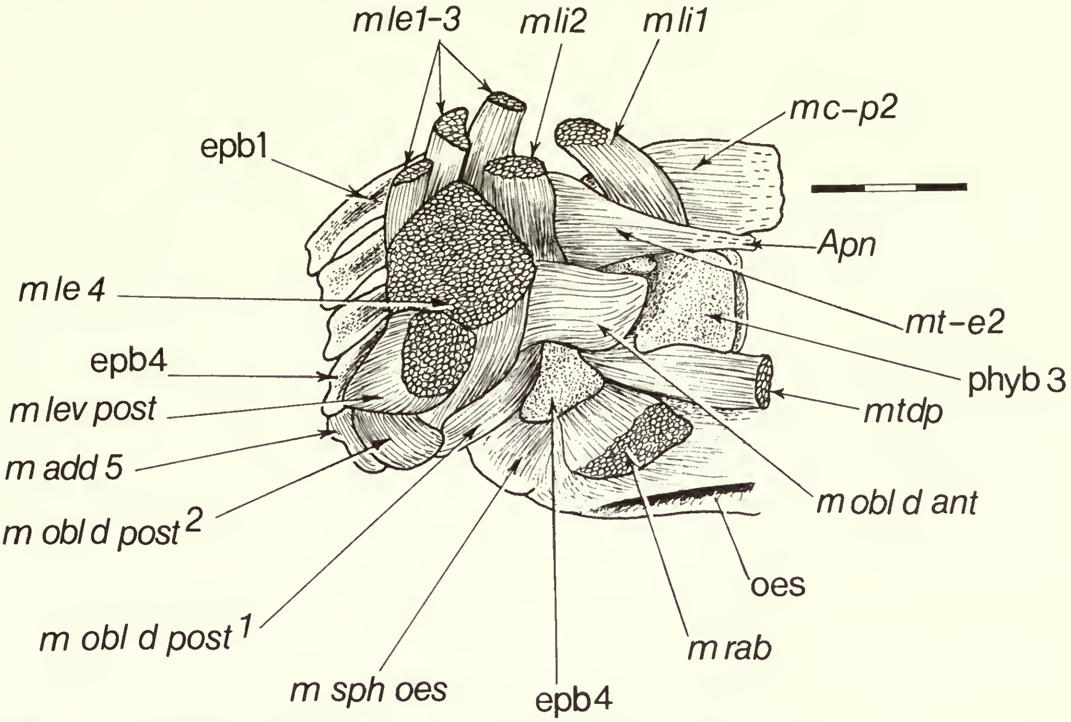

Fig. 24 *Hemichromis fasciatus*. Dorsal gill-arch musculature, in dorsal view. The *m. transversus pharyngobranchialis* 2 is not visible since, in this view, it lies below the *m. cranio-pharyngobranchialis* 2 muscle (1976.11.12:138–41).

jaw' which they cite as a synapomorphy for the cichlids, embiotocids and labrids; it is clearly a feature already manifest in several cichlids.

In *Hemichromis fasciatus* the medial division of the *m. obliquus dorsalis posterior* is a moderately substantial muscle, but is noticeably less voluminous than the anterior division of the *obliquus* complex.

On Stiassny's reckoning (1982:436; figs 7 & 8), the origins of the *mm levatores externi* and *interni* of *Hemichromis* are displaced caudally, and according to her a well-developed hyomandibulad shell is lacking in this taxon. In both these features Stiassny considers *Hemichromis* to be comparable with *Cichla,* certain other Neotropical taxa, and the Madagascan etropline *Paratilapia*. She also considers the features to be plesiomorphic ones.

The peculiarly developed and unique hyomandibulad shell, or rather hyomandibulad pit was discussed on p. 142. No comparable structure is present in *Paratilapia, Cichla* or the other Neotropical taxa listed by Stiassny, namely *Petenia, Chaetobranchus* and *Crenicichla.*

When viewed laterally the apparent origin of the *levatores externi* and *interni* muscles in *Hemichromis* begins at a line drawn vertically through the middle of the anterior facet of the hyomandibular head, and continues backward to a line drawn though the posterior hyomandibular facet. In other words, the origins of these muscles occupy an area comparable with that illustrated by Stiassny (1982: fig. 8) for *Astatotilapia,* which species she considers to have an 'anterior' area of origin for these muscles.

In actual terms rather than apparent ones, the *mm levatores externi* 1–4 in *Hemichromis fasciatus* originate mainly from the roof and sides of the hyomandibulad pit; the mediocaudal part of the fourth muscle, however, originates from the anterior boundary wall of the deep awning (see p. 142). The *mm levatores interni* 1 and 2 also originate from the hyomandibulad pit, which occupies an area almost identical with the triangular area of origin for the levator muscles in *Astatotilapia* illustrated by Stiassny (1982: fig. 8).

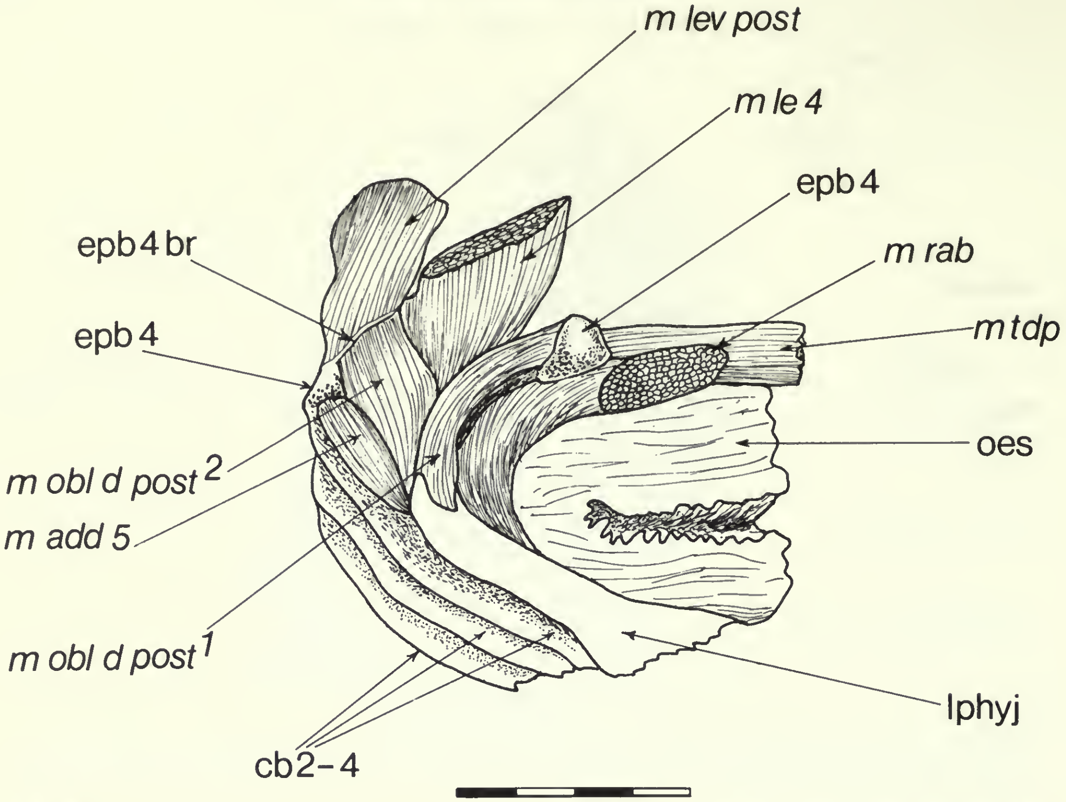

Fig. 25 *Hemichromis fasciatus.* Dorsal gill-arch muscles viewed from behind and a little ventrally. The *m. levator posterior* has been reflected laterally and somewhat anteriorly.

Thus, there would seem to be no grounds for considering the situation in *Hemichromis,* apart from the pit-like hyomandibulad shell, as being significantly different from that in *Astatotilapia,* nor is it like the presumed plesiomorph condition in *Cichla* and the other Neotropical taxa mentioned by Stiassny.

LATERAL AND VENTRAL GILL-ARCH MUSCLES

These muscles in *Hemichromis* were not studied in detail except to compare certain elements with those in *Cichla,* which Stiassny (1982: 437–442) described and commented upon, and others which were noted by Vandewalle (1971:271, fig. 5) in his account of *Hemichromis fasciatus.*

Stiassny (1982: 438) noted that in *Cichla ocellaris* certain elements of the 'muscular sling' associated with the lower pharyngeal jaw departed from the assumed modal cichlid condition seen in *Astatotilapia. Hemichromis,* in contrast, departs but slightly in these features from the *Astatotilapia* condition (Anker, 1978; Stiassny, 1982). For example, the B branch of the *m. pharyngocleithralis externus* in *Hemichromis* is much narrower below its division into the branches attaching to the lower pharyngeal bone and the fourth ceratobranchial respectively, and its musculose part is relatively much shorter than in *Cichla ocellaris.*

The *pharyngohyoideus* in *Hemichromis,* both in its insertion on the lower pharyngeal bone, and in its relationships with the tendons of *pharyngocleithralis externus* B, is like that muscle in *Astatotilapia.* Anteriorly it inserts along the dorsal surface of the urohyal, and terminates by inserting on the well-developed urohyal spine.

Vandewalle (1971:271; fig. 5) notes, apparently as a unique condition among the two African and three Neotropical cichlids he studied, that the *m. obliquus ventralis* 3 and the *m. rectus ventralis* insert on the third hypobranchial *via* '... un tendon en fer à cheval' (Anker's [1978] semicircular ligament). Vandewalle's figure is somewhat misleading since it shows both muscles apparently inserting entirely on the ligament. That is so for the *rectus ventralis*, but the greater part of the *obliquus ventralis* 3 inserts directly onto the hypobranchial, to which bone the semicircular ligament is also attached. Indeed, it is only the medial margin of *obliquus ventralis* 3 which is associated with the ligament.

Involvement of these two muscles with a semicircular ligment is by no means unique to *Hemichromis*. Such an association is present, among African taxa, in *Serranochromis* (*Sargochromis*) *mellandi, Tilapia sparrmani, Astatotilapia burtoni, A. elegans, Aulonocranus dewindti, Rhamphocromis longiceps, Trematocara unimaculatum, Hemibates stenosoma, Thoracochromis buysi* and *Chromidotilapia guentheri* (personal observations; also Anker, 1978 for *Astotilapia elegans*). The tilapiine species examined by Goedel (1974), *Tilapia tholloni, Oreochromis niloticus* and *Sarotherodon melanotheron,* show a similar arrangement.

Only one Madagascan species, *Paratilapia polleni,* could be dissected; it too shows the same arrangement as that in the species listed above. So too do two of the Neotropical species I examined, *Acarichthys heckeli* and *Chaetobranchus flavescens*. In two other Neotropical taxa, *Cichla ocellaris* and *Crenicichla saxatilis,* however, the insertions of *obliquus ventralis* 3 and *rectus ventralis* 4 are quite different, and resemble the condition found in the serranid *Serranus cabrilla*.

In *Cichla* there is no semicircular ligament; *obliquus ventralis* 3 is an elongate as opposed to a short muscle, and it inserts directly onto hypobranchial 3. *Rectus ventralis* 4 is also elongate, runs parallel and medial to *obliquus ventralis* 3, and also inserts on hypobranchial 3, but by a long and discrete tendon which passes through part of *obliquus ventralis* 3 before it attaches, independently, onto the hypobranchial.

The arrangement of the muscles in *Crenicichla* is essentially similar, but the *rectus ventralis* 4 is shorter.

Intrafamilial variability in the arrangement of these muscles also occurs, but is less extreme than that existing between *Cichla* or *Crenichichla* and the other species noted above. For example, in *Bathybates vittatus,* although much of the *obliquus ventralis* 3 inserts directly on the hypobranchial, and part also attaches to the ligament, there is a substantial, medially directed division which joins a similar division from its antimere in a median aponeurosis; part of this aponeurosis attaches to the semicircular ligament. The *rectus ventralis* 4, like that in the other species, inserts onto hypobranchial 3 entirely *via* the semicircular ligament.

Since in *Cichla* the arrangement of these muscles and their insertions are like those in *Serranus,* it would seem that the presence in other cichlids of a semicircular ligament should be considered a derived condition. That interpretation is complicated, at least for the moment, by the presence in *Perca fluviatilis* of a semicircular ligament and muscle insertions exactly like those in cichlids.

A semicircular ligament is present in the pomacentrid *Abudefduf leucozona,* in the labrid *Centrolabrus trutta* and in the embiotocid *Cymatogaster aggregata*. In these taxa, however, there are differing types of muscle association with the ligament, none of which is represented in the cichlids examined. For example, in the pomacentrid and the labrid only *rectus ventralis* 4 inserts on the semicircular ligament, whilst in the embiotocid, although some part of both it and *obliquus ventralis* 3 insert in that way, the overall arrangement of the ventral gill-arch musculature differs greatly from that in the cichlids, pomacentrids and labrids.

Clearly, a lot more comparative data derived from cichlids and from percoid outgroups are needed before the transformational polarity of these various conditions can be established. It is possible, for example that the *Cichla-Crenicichla* situation is not, as it now seems, the plesiomorphic one. It might be a secondary reversion to the 'primitive' state and hence can be treated as a derived feature.

Buccopharyngeal and swimbladder anatomy

No hanging pad (see Trewavas, 1974: 389–391; Greenwood, 1983: 265–267) of the type found in *Chromidotilapia* is present in any of the *Hemichromis* species examined. As in most African cichlids, however, the pharyngeal epithelium immediately anterior and somewhat lateral to the upper pharyngeal bones is noticeably thickened. In at least some *Hemichromis* the thickening is more pronounced than is usual in most other African cichlids, and the region could be described as having the appearance of an incipient hanging pad. Unfortunately, this region of the pharynx is easily affected by preservation and by the immediate post-mortem history of the specimen, especially temporary dehydration; a once substantially pachydermatous pad can be much reduced in size. Similar factors may also affect the degree to which a sulcus is apparent between the pad-like region and the less thickened tissues of the posterior buccal roof.

A deep sulcus, like that in *Chromidotilapia,* is present in *Hemichromis fasciatus,* but is either absent or represented by a faint transverse depression in specimens of *H. bimaculatus, H. letourneauxi, H. lifalili* and *H. paynei* examined. When a deep sulcus is present it is interrupted in the midline so that, effectively, there are distinct left and right sulci.

The frenum connecting the suspensorium with the first gill-arch inserts high on that arch, well above the epi-ceratobranchial articulation (see Trewavas, 1973: 18; 1974:391). This is apparently the common condition in African cichlids, although not in (?all) tilapiines (see Trewavas, 1973:18).

The thin-walled swimbladder in *Hemichromis fasciatus* is bilobed anteriorly from a point level with the posterior margin of the third centrum. Each lobe extends anteriorly to about the posterior margin of the second vertebra, and touches the Baudelot's ligament of its side. There is no posterior extension of the swimbladder beyond the limits of the visceral cavity. The transverse septum, which has a moderately large foramen ventrally, lies somewhat posteriorly in the bladder at a point about level with the pleural rib sixth from the end of the series.

Little has been published on swimbladder anatomy and morphology in cichlids (see Cichocki, 1976:115–116), but from personal observations the *Hemichromis* swimbladder would seem to be in no way unusual.

The phylogenetic status of *HEMICHROMIS*

The ultimate object of this paper was to review, in the light of new anatomical data, two questions. First, is *Hemichromis,* as Cichocki (1976:184) and Van Couvering (1982:fig. 11) have indicated explicitly, and others have suggested, a primitive African cichlid? Second: can one identify the sister-group for *Hemichromis*?

That *Hemichromis* is a substrate brooder (see Loiselle, 1979 for further details and references) would, perforce, give it a primitive status relative to any mouth-brooding taxon with which it shared a common ancestry. But, apart from its reproductive characteristics (which are rarely mentioned by authors who would rank *Hemichromis* as primitive) it is difficult to determine from previous accounts just why the taxon has been given its rating as a primitive African cichlid.

Neither Pellegrin (1903), Sauvage (1910), nor Regan (1922) undertook any detailed study of *Hemichromis* anatomy, and even Cichocki's (1976) opinion is weakened by his having only compared it with three other African genera. Van Couvering's (1982) work, too, is limited by the few cichlid out-groups she examined and by the few anatomical features which were taken into account. Finally, and most important, none of these authors clearly indicates their reasons for assigning *Hemichromis* to its plesiomorphic status within the family.

Assessing the various anatomical features discussed earlier, both in relation to other African cichlids and to those from the Neotropics, Asia and Madagascar, *Hemichromis* is seen to exhibit two clear-cut autapomorphies, namely the nature of the ethmopalatine articulation, and the development of a hyomandibulad pit. The absence of lateral ethmopalatine ligaments might be considered a third apomorphy, but this character could be correlated with the unusual ethmopalatine joint system in *Hemichromis.*

Besides its autapomorphic characters, *Hemichromis* has derived features which are shared with many other members of the family. For example, the cranial apophysis for the upper pharyngeal bones is structurally of the *Haplochromis* type, a character shared with numerous other African taxa but only one Neotropical species, *Cichla* (see Greenwood, 1978 for discussion of this feature). When compared with Neotropical species, *Hemichromis,* like other African taxa shows the derived condition of the *adductor arcus palatini* muscle extending onto the palatine bone (p. 156). In the gill-arch musculature, the association of the *obliquus ventralis* 3 and *rectus ventralis* 4 muscles with a semicircular ligament (p. 163) is a derived condition shared with a great number of African and Neotropical cichlids, and also with the single Madagascan species in which the muscles could be checked. The absence of a calyx (p. 145) is apparently a derived feature, and one which *Hemichromis* shares with some Neotropical taxa but with no other African species; it is very doubtful, however, if this feature can be treated as a true synapomorphy. The absence of a laterosensory canal through the anguloarticular bone is seemingly the only synapomorphic feature in *Hemichromis* having a very restricted occurrence outside the genus, otherwise being found only in *'Pelmatochromis' thomasi*. There are other features in *Hemichromis*, such as the glandular pseudobranch, the single coronal lateralis canal opening, edentulous vomer, and the single predorsal bone, which are very widely shared with other African and Neotropical taxa, and are represented in the plesiomorphic state only amongst the etropline cichlids of Madagascar and Asia.

The sum of these autapomorphic and synapomorphic features in *Hemichromis* is notable. What then of its plesiomorphic or supposedly plesiomorphic characters?

A derived character probably synapomorphic for African cichlids is the presence of an anteroventral palatomaxillary ligament (see p. 158; also Cichocki, 1976). This ligament is absent in *Hemichromis*, but that could be correlated with the peculiar ethmopalatine articulation in the genus; if that is so, then it cannot be ranked as a plesiomorphic feature for *Hemichromis*. The very slight extent to which, in *Hemichromis*, the *levator posterior* muscle of the dorsal gill-arches is associated with the horn of the lower pharyngeal bone (see p. 160), and the retention of some contact between the fourth *levator externus* muscle and the fourth epibranchial bone, are both plesiomorphic features. However, a similar situation obtains in several of the African taxa I examined (and also in *Cichla* [Stiassny, 1982; pers. obs.). The lack of a discrete shank spine on epibranchial 4, and the shape of that bone's quadrangular region (see p. 151), are, however, plesiomorphic features neither of which is so clearly exhibited in any other African taxon, even those in which the condition of *levator externus* 4 and the *levator posterior* muscles is comparable with that in *Hemichromis*.

The presence in *Hemichromis* of a definite articulation between the metapterygoid and the anterior flange of the hyomandibula is a plesiomorphy, but its expression here is less primitive than that of a sutural union between these bones, as is found in some Neotropical taxa (see p. 145). The absence of a calyx in *Hemichromis*, however, may well be an autapomorphy, one not recorded in any other African cichlid, but one which is known from some Neotropical species (see p. 146).

The occurrence of only four openings to the lateralis system in the lachrymal (p. 147) is another plesiomorphic feature (Cichocki, 1976; Trewavas, 1983:9; see also Greenwood, 1983) and one found in all Neotropical species as well as in *Etroplus* (Asia) *Paretroplus* and *Paratilapia* (both Madagascan). In African cichlids, four openings are present only in *Pseudocrenilabrus, Nanochromis, Pelmatochromis, Pterochromis, Thysia* and some *Pelvicachromis* species, as well as in certain *Oreochromis* species (Trewavas, 1983:9; pers. observations). Trewavas (*op. cit.*), however, considers that the condition in the *Oreochromis* species represents a secondarily derived state evolved from the usual five openings which characterize the great majority of African taxa.

Total vertebral counts in *Hemichromis* (25–28, mode 25), and the relative number of abdominal and caudal vertebrae (12–15 and 11–14 respectively), fall within the range considered as plesiomorphic for cichlids (see Stiassny, 1982:449). Again, similar counts and ratios are found in other African and in Neotropical species, although the figures for *Hemichromis* are in the lower and thus presumably least derived part of that range.

Zihler (1982:564) identifies the coiling pattern of the gut in *Hemichromis fasciatus* and *H. bimaculatus* as '. . . generalized or primordial', and of a type not found in any of the several other African species he studied, although it does occur in some Neotropical cichlids. Unfortunately, Zihler's review takes account of only one etropline genus (*Etroplus*) and does not include *Pelmatochromis, Thysia, Nanochromis, Pterochromis* or *Pseudocrenilabrus,* taxa which, for various reasons are thought to be 'primitive' members of the African cichlid radiation. Despite that limitation, however, Zihler's work clearly establishes that gut morphology in *Hemichromis* cannot be considered of a derived type.

Fin-ray counts and the nature of the underlying skeletal structures, both in the paired and unpaired fins of *Hemichromis* are shared with several taxa, especially African species. These features probably should be ranked as plesiomorphies, although a detailed analysis of their status has yet to be made. Whether or not the small process on the second postcleithrum in *Hemichromis* can be considered a plesiomorphy is also indeterminable (see p. 154).

In summary it would seem that the majority of plesiomorphic characters in *Hemichromis* are widely symplesiomorphic in cichlid fishes, and that none can be used to categorize *Hemichromis* as an especially 'primitive' taxon within the family. Granted its reproductive biology (see p. 164) must place it amongst the less derived members of the family. But within these substrate brooding species (which, as a group, cannot on that basis, be taken to have any phyletic coherence) *Hemichromis* does not exhibit an especially high number of plesiomorphic traits. In contrast, it would appear to have a greater number of autapomorphic features than do the other African substrate brooders.

At least for the moment there would seem to be no grounds for ranking *Hemichromis* as the most primitive living non-tilapiine cichlid taxon in Africa, as was recently implied by Van Couvering (1982). Even Cichocki's (1976:184) assessment that 'The primitive position estimated for *Hemichromis* is in complete accord with the assessment of Pellegrin . . . ' would seem to be somewhat over emphatic, although valid with respect to its spawning habits. But then, there are other substrate brooders amongst the non-tilapiine African cichlids, and none of those has as many derived features as does *Hemichromis*.

The problem of recognizing a sister group for *Hemichromis* is complicated by the genus exhibiting what, in that context, are a predominance of autapomorphies and symplesiomorphies, a difficulty frequently faced by those who work on cichlid fishes. There are, of course, several synapomorphic features, but these are so widely shared as to be useless except in recognizing sister-groups at the highest hierarchial levels. Synapomorphic features of a more circumscribed kind are difficult to identify.

One outstanding autapomorphy for *Hemichromis* lies in the precise nature of its ethmopalatine articulation. Basically, however, the articulation can be classified in one of the two major articulation types found in the Cichlidae. That is, a single rather than a double contact between the palatine and the ethmoid complex.

The majority of African cichlids have a double articulation (pp. 131–132), the palatine contacting the lateral face of the lateral ethmoid anteriorly near or on its suture with the vomer, and posteriorly with a ventrally directed, drum-like facet on the lateral ethmoid near that bone's median margin (see p. 139). Judging from outgroup comparisons with other percoids (eg *Serranus, Lates* and *Perca*) and with sub-perciform taxa as well, this articulation type must be considered plesiomorphic (see also Cichocki, 1976:73).

In sharp contrast to the African taxa, most Neotropical species have only the anterior palatoethmoid articulation; the posterior laminar process of the palatine (if developed) has no contact with the lateral ethmoid.

If the double articulation is taken to be plesiomorphic, then many Neotropical taxa show the derived condition, as do a few African taxa (including *Hemichromis*). Furthermore, since both the derived single articulation and the plesiomorphic double one occur in Neotropical and African cichlids, and both occur in the Madagascan taxa, it could be argued that the existence of the two types indicates an early dichotomy in the phylogenetic history of the family.

Unfortunately for that hypothesis there is a suggestion that the derived single articulation may have evolved more than once within the Cichlidae. Evidence for that possibility stems chiefly from the occurrence of both types within the African genus *Bathybates* of Lake Tanganyika. Three *Bathybates* species have a single articulation, two have the typical double type, and one species, *B. ferox,* has both types, with the double joint occurring more frequently than the single one.

This possibility of repeated and independent evolution is reinforced by the occurrence of the single articulation type in one species of *Sarotherodon, S. linelli,* a member of a tilapiine genus in which otherwise only the double articulation is present. Intriguingly, and perhaps significantly for the thesis of independent evolution, *Sarotherodon caroli,* an apparently close relative of *S. linelli* (Trewavas *et al,* 1972:52) living sympatrically with it in the isolated Cameroonian crater lake Barombi Mbo, has a double articulation.

Thus, on the basis of current information, I do not think one can safely interpret the *Hemichromis* ethmopalatine articulation as indicative of the genus being more closely related to taxa with a single articulation than to those with the double type.

Regan's (1922) implied close relationship of *Hemichromis* and *Haplochromis* apparently was based solely on the two taxa having a *Haplochromis*-type of neurocranial apophysis, and was influenced by his belief in the character as an important indicator of phylogenetic relationship (see discussion in Greenwood, 1978). There are no other synapomorphies shared only by *Hemichromis and Haplochromis* (the latter broadly conceived as it was by Regan; see Greenwood, 1979). Neither are there any synapomorphies shared only with particular members of the broader but non-phylogenetic haplochromine concept currently used to embrace those African cichlids with a *Haplochromis*-type of apophysis (see Greenwood, 1978; 1979). Furthermore, it would seem inadvisable to consider the possession of a *Haplochromis*-type apophysis as indicative of close phyletic relationship (Greenwood, 1978). In itself, an apophysis of that type can be considered derived relative to the *Tilapia*-type, but a *Haplochromis* apophysial type could have evolved, independently, on more than one occasion; relevant ontogenetic information is contained in Ismail *et al,* 1982.

Hemichromis, it will be recalled, has been considered a close relative of the extinct African genus *Palaeochromis* (Sauvage, 1907, 1910). The grounds for that alliance, namely body-form, vertebral counts and oral tooth morphology, cannot be treated as critical in a phylogenetic context. Body form can be considered only a matter of overall similarity, and in this particular instance a similarity repeated many times over in different lineages; the vertebral counts in both genera are plesiomorphic features, and the supposed similarity in oral dentition can be discounted by Van Couvering's recent examination of the two genera (Van Couvering, 1982:93). Sauvage (1910:52) also believed that *Palaeochromis* linked *Hemichromis* with the Neotropical genus *Acara* (a relationship for *Hemichromis* first postulated by Pellegrin, 1903); in this context, *Acara* should probably be read as *Aequidens.* Like Pellegrin, Sauvage gave no reasons for his suppositions, and the proposal must also have been made on the basis of overall similarity. I can find no synapomorphies suggesting even a moderately distant relationship between either *Hemichromis* and *Palaeochromis* or *Hemichromis* and any Neotropical taxon.

Recently, Loiselle & Welcomme (1972:53 *et seq*), when considering the relationship of their new West African genus *Thysia,* thought (*op. cit.*:57) it reasonable to consider *Thysia* '... as a rather generalized cichlid most closely allied to the *Hemichromis bimaculatus-Pelmatochromis thomasi* group within *Hemichromis* sensu lato'. They go on to comment that '... These two groups, together with the *Hemichromis fasciatus* species group within *Hemichromis,* can be considered an oligophyletic assemblage comparable to *Tilapia* sensu lato. A comparable arrangement seems applicable to the *Nanochromis-Pelvicachromis-Chromidotilapia* group of cichlids which, on the basis of evidence presented in Thys (1968*a*), represent a common evolutionary assemblage. We therefore propose two further groups of cichlids, the hemichromine cichlids, consisting of *Hemichromis* sensu lato and *Thysia,* and the pelmatochromine cichlids consisting of the genera *Nanochromis, Pelvicachromis* and *Chromidotilapia'.*

There are several apparently phylogenetic statements made in those quotations, but none would seem to stand up to closer examination.

Loiselle and Welcomme's association of *Hemichromis* with *Thysia* is not based on any synapomorphic characters (see Loiselle & Welcomme, 1972:53–54; and compare with pages 164–165 above). Once again 'affinities' were based on symplesiomorphies, including spawning habits. In this instance, the number of listed similarities between *Hemichromis* and *Thysia* are outnumbered by their dissimilarities (Loiselle & Welcomme, 1972:56), thus making it difficult to understand, without further justification, why Loiselle and Welcomme concluded that the two genera were 'closely allied' or why the two taxa should form a distinct subgroup within the African assemblage.

The suggestion that *'Pelmatochromis' thomasi* might be closely related to *Hemichromis* (see quote above) was initiated by Thys van den Audenaerde (1968:382), mainly on the grounds of its coloration and reproductive behaviour being much like that in *H. bimaculatus* (*sensu lato* in the light of Loiselle's [1979] later revision of *Hemichromis*).

'*Pelmatochromis*' *thomasi* has a typical double ethmo-palatine articulation (see p. 139), lacks a ventral vomerine support for the palatine, has both lateral and anteroventral palato-ethmoidal ligaments, and lacks a hyomandibulad pit. In other words, it shares none of the principal apomorphies characterizing *Hemichromis*. However, it does share one derived feature with that genus, namely the absence of a latero-sensory canal running through the anguloarticular, a presumed apomorphy not recorded in any other cichlid. On that feature, and that feature alone, *'Pelmatochromis' thomasi* would appear to be the most likely candidate for consideration as the sister taxon to *Hemichromis*.

The use of a 'loss' character as a synapomorphy must be treated with considerable circumspection, especially when, as in this case, it is not backed by other synapomorphies. Thus, even though there are no contraindicative characters, this postulated sister-group relationship should be considered as a very tentative hypothesis. The possibility that it might be corroborated by ethological evidence (see Thys van den Audenaerde, 1968) requires further investigation but would be well worth pursuing. At present there are insufficient data to establish the polarity of such features; the fact that *'P'. thomasi* and the *Hemichromis* species are substrate brooders is of no value in establishing relationships since that is a plesiomorphic character.

Although I have used the binomen '*Pelmatochromis' thomasi,* the generic relationships of the species are currently *incertae sedis.* Trewavas (1973:14) specifically excludes *thomasi* from *Pelmatochromis.* On the basis of those characters she used to redefine the genus I would agree with its exclusion, and likewise cannot include the species in either *Pelvicachromis* or *Chromidotilapia,* the other elements of the earlier *Pelmatochromis* generic concept. Rather than confuse the issue further by creating a new genus for *thomasi,* and pending a phylogenetically orientated revision of *Pelmatochromis, Pelvicachromis* and *Chromidotilapia,* I chose to refer to the species as *'Pelmatochromis' thomasi.* In that way both its uncertain generic position and its overall superficial phenetic 'relationships' can be indicated.

If *'Pelmatochromis' thomasi* and *Hemichromis* are sister taxa, the question then arises of their relationship to other African groups. For the moment there are few anatomical or morphological data indicating where that relationship might lie. One character, which might provide an escape from that dilemma, but only after much more research, concerns the nature of circulus patterns on the scales of *Hemichromis.* Trewavas (1973:14; fig. 10) drew attention to the peculiar 'gothic arch' pattern of the central circuli in the posterior field of the body scales in *Hemichromis* and *'Pelmatochromis' thomasi,* and the presence of a similar pattern on at least some scales in other West African taxa, *viz: Tilapia ruweti, Pelmatochromis buettikoferi, P. ocellifer, P. nigrofasciatus* and young specimens of *Pterochromis congicus.* Unfortunately, little is known about the finer morphology of the scales in most cichlid fishes, and the primitive or derived status of the 'gothic arch' pattern is undetermined. A preliminary survey of Neotropical and African species in the BMNH collections indicates that the pattern occurs in 10 of the 116 Neotropical species examined (sometimes in one but not all species of a genus), that it is absent in all but three African tilapiine species, and that it occurs in some non-cichlid taxa as well (e.g. *Serranus cabrilla*).

From those data I would be chary of using the 'gothic arch' pattern alone to suggest relationships between the African species in which it occurs, the more so since, except for *Hemichromis* and *'Pelmatochromis' thomasi,* there are no congruent synapomorphies known to be shared only by those taxa.

Parenthetically, it is interesting to record that Thys van den Audenaerde (1968), expressed doubts about the congeneric status of *H. fasciatus* and *H. bimaculatus,* mainly because the latter has much smaller canine-like teeth in its oral dentition. Although, because of their various uniquely shared specializations, it would be difficult to doubt the close relationship of the two species, there are other features, especially vertebral numbers (p. 155) and the shape of the premaxilla (p. 148) which suggest the possibility of a *fasciatus-bimaculatus* lineage dichotomy within the genus. Thys van den Audenaerde (1968:372) also treated the species *cerasogaster* Boulenger, 1898 as a member of the genus *Pelmatochromis*. My anatomical studies would, however, fully confirm Loiselle's (1979:88) inclusion of that species in *Hemichromis*.

In the latter paper Loiselle (*op. cit.*: 94) develops further the idea, first aired by Loiselle & Welcomme (1972), of a close relationship between *Thysia* and *Hemichromis*. He argues for relationship on the grounds that *H. cerasogaster* has the most plesiomorphic, that is multi-seriate, dental pattern of all *Hemichromis* species, and that in this feature there is a close resemblance between it and *Thysia*. Since, quite explicitly, this proposal is based on a symplesiomorphy it adds nothing to the other arguments, also based on symplesiomorphies, which were put forward earlier by Loiselle & Welcomme (1972).

Finally, mention must be made of the most recent view on a possible African sister-group relationship for *Hemichromis*, albeit one on a taxonomically broader scale than any put forward previously. This is expressed in Van Couvering's cladogram of African (and Madagascan) cichlid relationships (Van Couvering, 1982:fig. 11). Here, but without any detailed reasoning given in the text, or synapomorphies included in the cladogram, *Hemichromis* is shown as the sister group of a *Pseudocrenilabrus* plus a *Haplochromis* lineage. *Haplochromis* in this context is apparently taken to include all those African taxa which Regan (1920; 1922 and later papers; see Greenwood, 1978) had described as having a *Haplochromis*-type of pharyngeal apophysis (see Van Couvering, 1982:17). *Pseudocrenilabrus*, however, is restricted to that genus alone. Again, I can find no synapomorphies to corroborate Van Couvering's grouping, and she offers none herself.

Apart from Pellegrin's (1903) and Sauvage's (1910) suggestion of close resemblance between *Hemichromis* and *Acara*, there have been no published indications of a possible relationship between *Hemichromis* and any Neotropical genus or generic group.

To the best of my knowledge, the monophyly of the Neotropical cichlids has not been established. Nor, for that matter has the monophyly of the African taxa been established either. However, Cichocki (1976:74) noted in the few African taxa he studied, but not in any of the Neotropical or Madagascan species, that the *adductor arcus palatini* muscle extends forward to insert on the palatine as well as on the pterygoid bones. I can now confirm that there is an anterior extension of this muscle in all the African taxa I examined (see p. 156). Since the muscle does not extend forward in any of the outgroup taxa examined by Cichocki or myself, there is a strong possibility that it is not only a derived feature but a synapomorphy indicating a monophyletic origin for the African species.

If that is so, then *Hemichromis* ultimately shares a common ancestry with all other African species (The Neotropical *Cichla*, despite its *Haplochromis*-type pharyngeal apophysis [see Regan, 1920], is excluded). Certainly, when other apomorphic features are taken into account, *Hemichromis* shows no close relationship with any Neotropical taxon, despite the fact that a single and anterior ethmopalatine articulation is commoner amongst Neotropical than it is amongst African taxa (see p. 139). The similarities which do exist between *Hemichromis* and the Neotropical cichlids (eg. breeding behaviour, isomorphic or weak sexually dimorphic coloration, four-pored lachrymal bone, morphology of the fourth epibranchial bone) are all symplesiomorphies.

To summarize, it would seem that, apart from *'Pelmatochromis' thomasi*, none of the previously suggested sister-group relationships for *Hemichromis* meet the requirements necessary to establish, unequivocally, the taxon's phyletic rather than its superficial phenetic affinities. The previously suggested relationship of *Hemichromis* with *'Pelmatochromis' thomasi* was based on features whose phyletic value cannot be assessed (*ie* coloration and breeding behaviour). The current suggestion is based on a single synapomorphy, and a 'loss' feature at that (albeit one which, seemingly has not been lost in any other cichlid, and which is rarely absent in other percoids).

Conclusion

On the evidence currently available, *Hemichromis* would seem to be a fairly isolated lineage within the radiation of African cichlids, of which it is phylogenetically a part. The lineage is recognizable on the basis of at least two autapomorphic features. Its sister group, with which it shares a single synapomorphy, is the taxon *'Pelmatochromis' thomasi*, a species whose generic placement is at present undecided.

Hemichromis exhibits several primitive features which, although retained in many Neotropical taxa, are lost in the great majority of African species. It does, however, share one derived feature with, if not all, then at least the majority of African taxa, and shows none which might suggest a closer relationship with the Neotropical rather than with the African taxa.

Although *Hemichromis* must, on several features, be ranked with primitive African members of the family it cannot be considered the most primitive member of that subgroup. The relationships of *Hemichromis* (+ *'Pelmatochromis' thomasi*) amongst the more primitive African cichlids are still undetermined.

Acknowledgements

My warmest thanks go to Gordon Howes, not only for his painstaking efforts in producing the figures illustrating this paper, but for the many other ways in which he has so freely given of his help. To Bernice Brewster I am indebted for help with numerous curatorial tasks, and for the innumerable radiographs and alizarin transparencies she has made. Miss Anna Hawkins, a vacation student in the Freshwater Fish Section, helped me immensely by studying and recording scale patterns in a large number of specimens; to her go my warmest thanks as well. Finally, I acknowledge my gratitude to Dr Gareth Nelson (American Museum of Natural History) and to Dr Thys van den Audenaerde (Koninklijk Museum voor Midden Afrika, Tervuren) who lent specimens and allowed me to carry out dissections on some of them.

References

Aerts, P. 1982. Development of the musculus levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae). A discussion on the shift hypothesis. *J. Morph.* **173:** 225–235.

Anker, G. Ch. 1978. The morphology of the head muscles of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **28:** 234–271.

Barel, C. D. N., Witte, F. & van Oijen, M. J. P. 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **26:** 163–265.

Boulenger, G. A. 1901. *Les poissons du bassin du Congo*. Publ. État. indep. Congo. Bruxelles.

Cichocki, F. 1976. *Cladistic history of cichlid fishes and reproductive strategies of the American genera.* Ph.D. thesis, University of Michigan, Ann Arbor.

Goedel, W. 1974. Beiträge zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae: Teleostei). *Zool. Jb. (Anat.)* **92:** 220–274, 321–383.

Greenwood, P. H. 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bull. Br. Mus. nat. Hist.* (Zool.) **33:** 297–323.

—— 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bull. Br. Mus. nat. Hist.* (Zool.) **35:** 265–322.

—— 1983. The *Ophthalmotilapia* assemblage of cichlid fishes reconsidered. *Bull. Br. Mus. nat. Hist.* (Zool.) **44:** 249–290.

—— 1984. The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers. *Bull. Br. Mus. nat. Hist.* (Zool.) **47** (4): 187–239.

Ismail, M. H., Verraes, W. & Huysseune, A. 1982. Developmental aspects of the pharyngeal jaws in *Astatotilapia elegans* (Trewavas, 1933) (Teleostei: Cichlidae). *Neth. J. Zool.* **32:** 513–543.

Johnson, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. *Bull. Scripps Instn. Oceanogr.* **24:** 1–114.

Kaufman, L. S. & Liem, K. F. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): Phylogeny, ecology and evolutionary significance. *Breviora* no. 472:1–19.

Liem, K. F. & Greenwood, P. H. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. *Am. Zool.* **21:** 83–101.

—— **& Osse, J. W. M.** 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Am. Zool.* **15:** 427–454.

Loiselle, P. V. 1979. A revision of the genus *Hemichromis* Peters 1858. *Annls. Mus. r. Afriq. Cent.* ser. 8vo. Zool. no. 228: 1–124.

—— **& Welcomme, R. L.** 1972. Description of a new genus of cichlid fish from West Africa. *Revue Zool. Bot. afr.* **85:** 37–58.

Pellegrin, J. 1903. Contribution a l'étude anatomique biologique et taxonomique des poissons de la famille des cichlidés. *Mem. Soc. zool. Fr.* **16:** 41–402.

Regan, C. T. 1920. The classification of fishes of the family Cichlidae-I. The Tanganyika genera. *Ann. Mag. nat. Hist.* (9) **5:** 33–53.

—— 1922. The classification of the fishes of the family Cichlidae.–II. On African and Syrian genera not restricted to the Great Lakes. *Ann. Mag. nat. Hist.* (9) **10:** 249–264.

Sauvage, H. E. 1907. Sur des poissons de la famille des Cichlides trouvés dans les terrain tertiare de Guelma. *C. r. hebd. Séanc. Acad. Sci. Paris,* **145:** 360–361.

—— 1910. Les poissons des marnes sulfogypseuses de la vallée de la Seybouse. *Matériaux carte géol. d'Algerie: Paléontologie,* Ser. 1 **4:** 50–54.

Stiassny, M. L. J. 1981*a*. Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika. *Bull. Br. Mus. nat. Hist.* (Zool.) **40:** 67–101.

—— 1981*b*. The phyletic status of the family Cichlidae (Pisces, Perciformes): A comparative anatomical investigation. *Neth. J. Zool.* **31:** 275–314.

—— 1982. The relationships of the neotropical genus *Cichla* (Perciformes, Cichlidae): a phyletic analysis including some functional considerations. *J. Zool. Lond.* **197:** 427–453.

Thys van den Audenaerde, D. F. E. 1968. A preliminary contribution to a systematic revision of the genus *Pelmatochromis* Hubrecht sensu lato (Pisces, Cichlidae). *Revue Zool. Bot. afr.* **77:** 349–391.

Trewavas, E. 1973. I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus;* on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bull. Br. Mus. nat. Hist.* (Zool.) **25:** 1–26.

—— 1974. The freshwater fishes of rivers Mungo and Meme and Lakes Kotto, Mboandong and Soden, west Cameroon. *Bull. Br. Mus. nat. Hist.* (Zool.) **26:** 329–419.

—— 1983. *Tilapiine fishes of the genera* ***Sarotherodon, Oreochromis*** *and* ***Danakilia.*** British Museum (Nat. Hist.), London.

—— **Green, J. & Corbet, S. A.** 1972. Ecological studies on crater lakes in west Cameroon. Fishes of Barombi Mbo. *J. Zool. Lond.* **167:** 41–95.

Van Couvering, J. A. H. 1982. Fossil cichlid fish of Africa. *Spec. pap. Paleon. Assn.* no. 29: 1–103.

Vandewalle, P. 1971. Comparison osteologique et myologique de cinq Cichlidae africains et sud-americains. *Annls. Soc. r. zool. Belg.* **10:** 259–292.

—— 1973. Osteologie caudale des Cichlidae (Pisces, Teleostei). *Bull. Biol. Fr. Belge.* **107:** 275–289.

Zihler, F. 1982. Gross morphology and configuration of digestive tracts of Cichlidae (Teleostei, Perciformes); Phylogenetic and functional significance. *Neth. J. Zool.* **32:** 544–571.

Manuscript accepted for publication 28 November 1984

British Museum (Natural History)

Tilapine fishes of the genera *Sarotherodon, Oreochromis* and *Danakilia*

Dr Ethelwynn Trewavas

The tilapias are cichlid fishes of Africa and the Levant that have become the subjects of fish-farming throughout the warm countries of the world. This book described 41 recognized species in which one or both parents carry the eggs and embryos in the mouth for safety. Substrate-spawning species, of the now restricted genus *Tilapia*, are not treated here.

Three genera of the mouth-brooding species are included though in one of them, *Danakilia*, the single species is too small to warrant farming. The other two, *Sarotherodon*, with nine species, and *Oreochromis*, with thirty-one, are distinguished primarily by their breeding habits and their biogeography, supported by structural features. Each species is described, with its diagnostic features emphasised and illustrated, and to this is added a summary of known ecology and behaviour. Conclusions on relationships involve assessment of parallel and convergent evolution. Dr Trewavas writes with the interests of the fish culturists, as well as those of the taxonomists, very much in mind.

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The Zoology Series is edited in the Museum's Department of Zoology

Keeper of Zoology : Mr J. F. Peake
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ISBN 0 565 05014 9
ISSN 0007 1498

Zoology series
Vol **48** No. 4 pp 173–300

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Echinoderms of the Rockall Trough and adjacent areas
2. Echinoidea and Holothurioidea

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Introduction

Eighteen species of echinoid and thirty-three species of holothurian are identified from a sampling programme conducted by the Scottish Marine Biological Association in the deep-sea areas lying to the west of Scotland and Ireland. Of these only one echinoid (*Aeropsis rostrata*) and 11 holothurians are unrecorded previously for the seas around the British Isles; these include two undescribed species of the holothurian order Apodida. The zoogeographical distribution and bathymetric range of each species are summarised as far as was previously known giving any range extension provided by the present records. Details are also provided on the biology of many species including their mode of reproduction. For certain echinoid species, the records demonstrate a broader bathymetric distribution for post larval stages than for the adult population. No such trend was evident amongst the holothurians. Holothurian species diversity was low on the west side of the Rockall Trough, an area where there is considerable current activity. This is in contrast to the pattern found for the Asteroidea and Ophiuroidea, which included several suspension-feeding species. There are few deep-sea suspension-feeding holothurian species, but apart from this the apparent scarcity of holothurians may be more appropriately attributed to unstable sedimentary conditions or possibly sampling bias.

The descriptive account of the echinoderm fauna in the samples, taken by the Scottish Marine Biological Association (SMBA) in the Rockall Trough area, is divided into two parts. The first part (Gage, Pearson, Clark, Paterson & Tyler, 1983) provides an introduction to the SMBA sampling programme, station data, records of the classes Crinoidea, Asteroidea and Ophiuroidea, bathymetric and geographic distributions in relation to previous records and details of the biology of many species. The second part provides similar information for the two remaining classes, the Echinoidea and Holothurioidea, the format following that of part 1.

List of Species

Class Echinoidea
  Order Cidaroida
    Family Cidaridae
      Cidaris cidaris (Linnaeus)
      Poriocidaris purpurata (Wyville Thomson)

  Order Echinothurioida
    Family Echinothuriidae
      Araeosoma fenestratum (Wyville Thomson)
      Calveriosoma hystrix (Wyville Thomson)
      Hygrosoma petersii (A. Agassiz)

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Station List

Only details of bottom sampling stations worked, yielding records of echinoids and holothurians, that are not listed by Gage *et al.* (1983) are given below.

Station No.	Date	Position (at mid-point of track on bottom if applicable)	Depth (m)
Benthic stations			
ES 110	22 Oct. 1976	54°41′N, 12°14′W	2886
ES 122	29 Jan. 1977	54°31′N, 12°31′W	2951
AT 130	7 April 1977	54°46′N, 12°19′W	*c.* 2900
ES 136	21 Feb. 1978	54°29′N, 12°18′W	2900
SBC 174	27 May 1980	54°44′N, 12°18′W	2885
SBC 188	15 Aug. 1981	54°41′N, 12°10′W	2876
AT 193	18 Aug. 1981	57°28′N, 11°08′W	616
AT 201	9 May 1982	57°22′N, 10°30′W	2180
ES 202	10 May 1982	57°22′N, 10°30′W	2180
ES 204	12 May 1982	54°40′N, 12°20′W	2904
SBC 205	31 July 1982	54°40′N, 12°15′W	2906
ES 206	1 Aug. 1982	54°40′N, 12°16′W	2900
ES 207	1 Aug. 1982	54°40′N, 12°11′W	2906
SBC 209	2 Aug. 1982	56°41′N, 09°00′W	416
SBC 210	2 Aug. 1982	56°40′N, 09°00′W	401
SBC 211	2 Aug. 1982	56°41′N, 09°00′W	402
SBC 212	2 Aug. 1982	56°43′N, 09°00′W	601
SBC 213	2 Aug. 1982	56°45′N, 09°06′W	841
SBC 214	2 Aug. 1982	56°45′N, 09°11′W	1062
SBC 215	3 Aug. 1982	57°02′N, 09°47′W	2001
SBC 216	3 Aug. 1982	57°19′N, 10°23′W	2200
ES 218	3 Aug. 1982	57°22′N, 10°24′W	2175
AT 219	3 Aug. 1982	57°25′N, 10°28′W	1991
SBC 220	4 Aug. 1982	59°05′N, 08°51′W	1608
AT 221	5 Aug. 1982	59°05′N, 08°55′W	1605
SBC 222	5 Aug. 1982	59°43′N, 07°10′W	1101
AT 223	5 Aug. 1982	59°41′N, 07°09′W	1075
SBC 224	6 Aug. 1982	60°10′N, 08°24′W	903
SBC 225	6 Aug. 1982	60°16′N, 06°56′W	1145
AT 226	6 Aug. 1982	60°16′N, 06°53′W	1118
SBC 227	6 Aug. 1982	61°00′N, 07°30′W	862
AT 228	10 Aug. 1982	57°01′N, 09°51′W	2026
AT 229	11 Aug. 1982	56°43′N, 09°30′W	1587
AT 230	11 Aug. 1982	56°44′N, 09°12′W	1210
Fishing station			
OTSB 51301	15 Feb. 1982	54°46′N, 12°14′W (starting position)	mean 2925

Sperosoma grimaldii Koehler
Family Phormosomatidae
Phormosoma placenta Wyville Thomson

Order Echinoida
Family Echinidae
Echinus acutus Lamarck
Echinus affinis Mortensen
Echinus alexandri Danielssen & Koren
Echinus elegans Düben & Koren
Echinus esculentus Linnaeus

Order Spatangoida
Family Aeropsidae
Aeropsis rostrata (Wyville Thomson)
Family Hemiasteridae
Hemiaster expergitus Lovén
Family Spatangidae
Brissopsis sp.
Spatangus raschi Lovén

Order Pourtalesioida
Family Pourtalesiidae
Pourtalesia jeffreysi Wyville Thomson
Pourtalesia miranda A. Agassiz
Echinosigra phiale (Wyville Thomson)

Class Holothurioidea
Order Dendrochirotida
Family Psolidae
Psolus pourtalesii Théel
Psolus squamatus (Koren)
Family Cucumariidae
Abyssocucumis abyssorum (Théel)

Order Dactylochirotida
Family Ypsilothuriidae
Ypsilothuria talismani talismani E. Perrier
Ypsilothuria bitentaculata attenuata R. Perrier
Echinocucumis hispida (Barrett)

Order Aspidochirotida
Family Synallactidae
Bathyplotes natans (M. Sars)
Benthothuria funebris R. Perrier
Paelopatides grisea R. Perrier
Mesothuria cathedralis Heding
Mesothuria lactea (Théel)
Pseudostichopus villosus Théel
Family Stichopodidae
Stichopus tremulus (Gunnerus)

Order Elasipodida
Family Deimatidae
Oneirophanta mutabilis mutabilis Théel
Family Laetmogonidae
Benthogone rosea Koehler
Laetmogone violacea Théel
Family Psychropotidae
Benthodytes lingua R. Perrier
Psychropotes depressa (Théel)
Psychropotes longicauda Théel

- Family Elpidiidae
    - *Peniagone azorica* von Marenzeller
    - *Peniagone diaphana* (Théel)
    - *Kolga hyalina* Danielssen & Koren

- Order Apodida
    - Family Synaptidae
        - *Labidoplax southwardorum* Gage
        - *Labidoplax similimedia* Gage
        - *Protankyra brychia* (Verrill)
    - Family Myriotrochidae
        - *Myriotrochus bathybius* H. L. Clark
        - *Myriotrochus giganteus* H. L. Clark
        - *Myriotrochus* sp.
        - *Prototrochus zenkevitchi* subsp.
        - *Prototrochus* sp. aff. *P. minutus* (Östergren)

- Order Molpadiida
    - Family Molpadiidae
        - *Cherbonniera utriculus* Sibuet
        - *Molpadia blakei* (Théel)
        - *Molpadia borealis* M. Sars

Systematic Account

A chart showing the station localities for all records is given in Fig. 1. More detailed charts for the most abundant echinoid and holothurian species in the central part of the Rockall Trough are given in Figs 2 and 5, respectively.

The classification of the class Echinoidea is based on that of Jensen (1982) and Smith (1981), although for brevity omitting some higher stages of Jensen's classification. That for the six orders of the Holothurioidea follows Pawson & Fell (1965) for the Dendrochirotida and Dactylochirotida, Hansen (1975) for the Elasipodida, Deichmann (1930) for the Aspidochirotida (except that *Zygothuria* is treated as a synonym of *Mesothuria*), Deichmann (1940) for the Molpadiida, and Clark (1907) for the Apodida. The classifications for the Aspidochirotida and Molpadiida proposed by Heding (1931, 1935, 1940, 1942) have, in most cases, been rejected and are not used. References to the size of animals, if given, refer to maximum test diameter or length of echinoids while the maximum body length of holothurians does not include retractile parts, such as the tentacles, tube feet or papillae that sometimes are not visible in fixed material.

Although all co-authors have been involved in the preparation of the text, taxonomic responsibility is taken by M.J. and J.D.G. for the echinoids, by J.D.G. for the holothurian order Apodida, and by D.S.M.B. for all remaining holothurians. Material of all species referred to in the present account will be deposited with the British Museum (Natural History).

Class **ECHINOIDEA**
Order **CIDAROIDA**
Family **CIDARIDAE**

Cidaris cidaris (Linnaeus, 1758)

See: Mortensen, 1903: 31–35, pl. 6, figs 6, 7, 8, pl. 8, figs 1, 3, 12, 14, 27, pl. 9, figs 3, 5, 7, 13–15, 20, 25, 27, pl. 11, figs 14, 26, 31 (as *Dorocidaris papillata*); 1927: 272–273, figs 149, 150(1, 2), 151, 152; 1928: 289–301, pl. 30, figs 3, 4, pl. 31, figs 1–10, pl. 67, fig. 5, pl. 72, figs 20–22.

SAMPLES. ES 23(1), AT 162(1), AT 193(1), AT 194(2), GT 7(3), GT 11(1), GT 12(1), GT 13(1), GT 14(1). [508–543 m to 934–1054 m]

DISTRIBUTION. Norwegian coast to the Cape Verde Islands and St Helena, also in the Mediterranean; 50–1800 m; on a variety of bottoms.

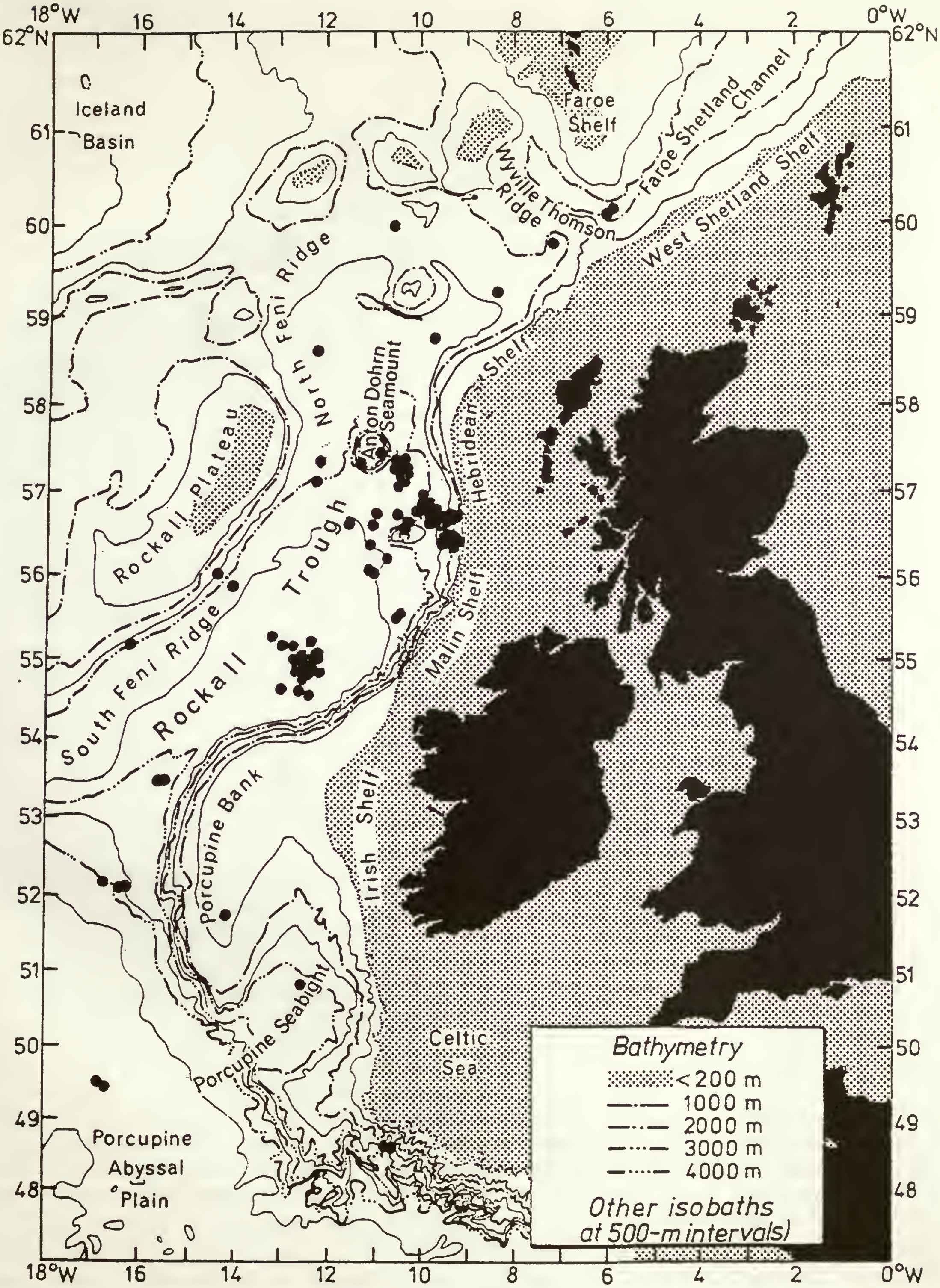
18°W
16
14
12
10
8
6
4
2
0°W
62°N
61
60
59
58
57
56
55
54
53
52
51
50
49
48
Iceland Basin
Faroe Shelf
Faroe Shetland Channel
Wyville Thomson Ridge
West Shetland Shelf
Feni Ridge
North
Anton Dohrn Seamount
Hebridean Shelf
Rockall Plateau
Rockall Trough
South Feni Ridge
Malin Shelf
Porcupine Bank
Irish Shelf
Porcupine Seabight
Celtic Sea
Porcupine Abyssal Plain
Bathymetry
< 200 m
1000 m
2000 m
3000 m
4000 m
Other isobaths at 500-m intervals)

Fig. 1 Bathymetric chart of the area sampled showing locations of stations yielding records of echinoids and holothurians.

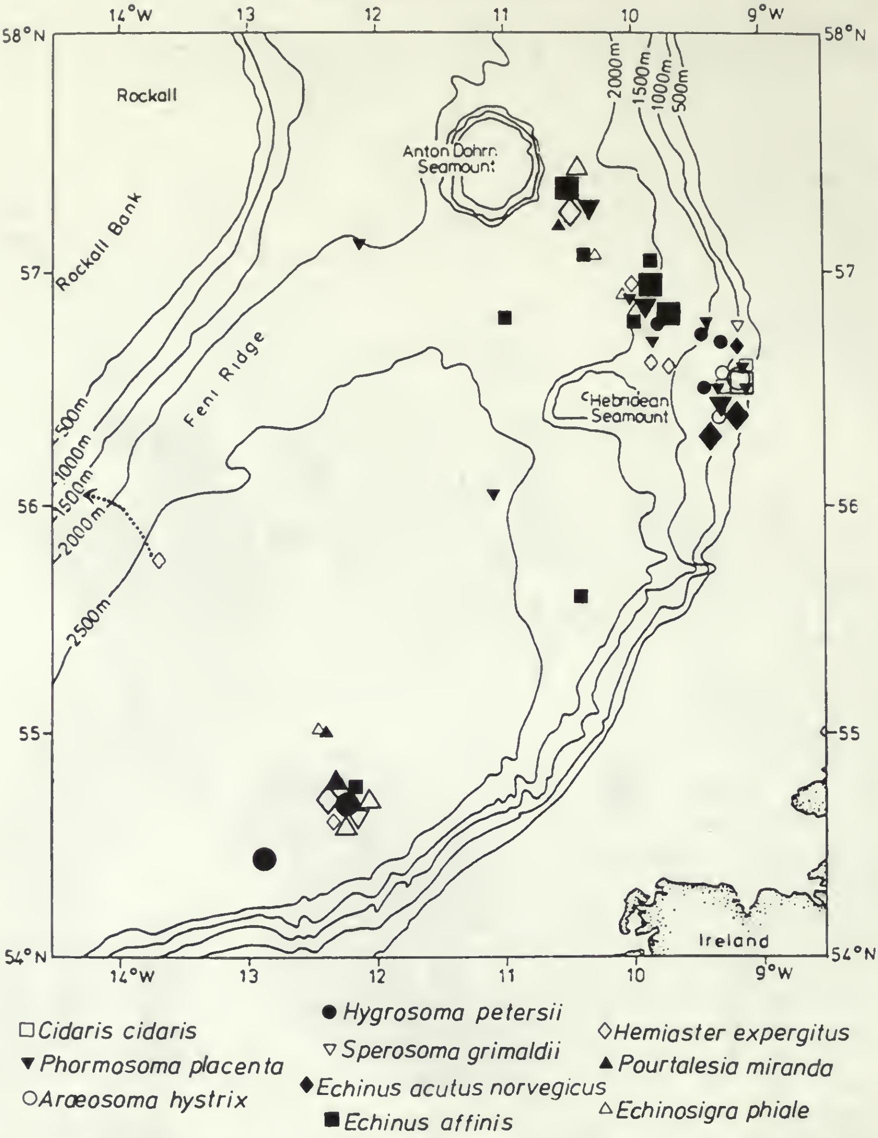
14°W
13
12
11
10
9°W
58°N
57
56
55
54°N
Rockall
Rockall Bank
Feni Ridge
Anton Dohrn Seamount
Hebridean Seamount
Ireland
2000m
1500m
1000m
500m
2500m
□ Cidaris cidaris
▼ Phormosoma placenta
○ Aræosoma hystrix
● Hygrosoma petersii
▽ Sperosoma grimaldii
◆ Echinus acutus norvegicus
■ Echinus affinis
◇ Hemiaster expergitus
▲ Pourtalesia miranda
△ Echinosigra phiale

Fig. 2 Chart of central part of Rockall Trough showing station locations for records of the ten most abundant echinoid species.

The present records are from the Hebridean Slope, the Porcupine Bank and Anton Dohrn Seamount and were all taken at depths less than 1000 m on bottoms of sandy ooze to fine calcareous sand. There are numerous previous records of this species, as *C. papillata* (Leske), from the waters west of the British Isles, particularly on the rough ground of the deeper fishing grounds such as the Rockall and Lousy banks. The deepest previous record in this area was that of Farran (1913) at 1293 m in the Porcupine Seabight.

REMARKS. The long, heavily built spines of this species, although usually recovered broken, often carried a variety of encrusting organisms that were attached, presumably beyond the range of the impressive battery of pedicellariae covering the test. It was also noted that the spines of small specimens (<40 mm test diameter) in some cases are more than three times as long as the diameter of the test.

The dietary items previously recorded for this species are summarised by De Ridder & Lawrence (1982).

REPRODUCTION. The sexes are separate; females produce numerous small eggs up to 110 µm in diameter (Tyler & Gage, 1984*b*). The larva is well known (Prouho, 1888; Mortensen, 1927), being a typical echinopluteus but possessing no postero-lateral arms.

Poriocidaris purpurata (Wyville Thomson, 1872)

See: Mortensen, 1903: 41–42, pl. 6, fig. 12, pl. 8, fig. 22, pl. 10, figs 1–2, 5, pl. 11, figs 3, 21; 1927: 274–275, figs 153, 154; 1928: 104–107, pls 1, 6, pl. 3, figs 3–5; Phelan, 1970: 16–17, pl. 10, figs 2–8, pl. 11, figs 1–6, pl. 12, figs 6, 7.

SAMPLE. GT 17(2), [1190–1296 m]

DISTRIBUTION. South and SW. of Iceland, northern Rockall Trough, off SW. Ireland, the Bay of Biscay, off the Canaries and in the Caribbean; 300–1800 m; on muddy bottoms.

This handsome species was first discovered by Wyville Thomson from a dredging by the *Porcupine* on the southern flank of the submarine ridge that was later named after him. The present record from the Hebridean Slope fits in well with the known distribution of this species which would appear to be geographically wider than that of *Cidaris cidaris*. Phelan (1970) in giving a bathymetric range of 750 to 1800 m did not include the shallower Icelandic records given by Einarsson (1948). However, it still seems likely that this species will be found to have a slightly deeper limit than that of *C. cidaris*.

Mortensen (1928) recorded bottom material and fragments of crustaceans in the gut contents of this species.

REPRODUCTION. The sexes are separate; *P. purpurata* produces large eggs up to 1400 µm in diameter suggestive of direct development (Mortensen, 1927; Tyler & Gage, 1984*b*).

Order **ECHINOTHURIOIDA**
Family **ECHINOTHURIIDAE**

Araeosoma fenestratum (Wyville Thomson, 1869)

See: Thomson, 1874; 741, pl. 63, figs 9, 10 (labelled as 9a), pls 66, 67 (as *Calveria fenestrata*); Agassiz, 1880; 29, pls 13–14 (as *Asthenosoma reynoldsii*); Mortensen, 1903: 72–75 pl. 11, fig. 8, pl. 12, fig. 33, pl. 14, figs 1, 8, 14, 17, 18, 24, 32; 1927: 283–284, fig. 160; 1935: 233–237, pls 29, 30, pl. 78, fig. 11.

SAMPLE. AT 194 (32). [631 m]

DISTRIBUTION. An upper bathyal species distributed throughout the North Atlantic excluding the Norwegian Sea; 148–990 m depth; on fine sand to soft mud.

This species, like many other Atlantic echinothuriids, was first discovered by Wyville Thomson from dredgings made by the *Porcupine* off Portugal. Subsequently, *A. fenestratum* has been recorded from several localities from the Denmark Strait to the deep waters off Scotland, Ireland and Brittany, and down the American side of the Atlantic to the Gulf of Mexico.

The present specimens were from a trawling on the fine shell-sand covering the Anton Dohrn Seamount, the depth of which approaches its previously known lower limit. However, the paucity of our records may reflect a lack of sampling effort at upper bathyal depths where this species would be expected to occur.

REMARKS. The size of the present specimens ranged from 130 to 190 mm in diameter. Their colour agreed in general with Mortensen's (1903, 1927) descriptions, all having a pale buff colour with a brownish or purple-brown colouration being concentrated along the ambulacra. The singular tetradactylous pedicellariae described and figured by Wyville Thomson (figured also by Mortensen, 1927, fig. 160) were not found. The tridentate pedicellariae on the largest specimens were markedly involute as figured by Mortensen (1903) with the blades measuring more than 3 mm. Another feature that has not previously been mentioned is that the aboral plates assume a chevron-like pattern as they approach the apex. This provides a useful additional feature to differences in test colouration and pedicellariae (see Mortensen 1903, pp. 52–53) in distinguishing this species from the closely similar *C. hystrix*.

De Ridder & Lawrence (1982) summarised the various gut contents, including bottom material, a gastropod, crustacean skeletons and woody fragments of terrestrial plants.

REPRODUCTION. Examination of the gonads shows the sexes to be separate; ripe oocytes that are occasionally in excess of 1200 μm in diameter were found together with two types of phagocytic tissue similar to those in *Phormosoma placenta*. A lecithotrophic or direct development of the fertilised egg to a benthic juvenile stage is predicted for this species (Tyler & Gage, 1984*b*).

Calveriosoma hystrix (Wyville Thomson, 1869)

See: Mortensen, 1903: 70–72, pl. 3; figs 1–2, pl. 11, figs 5, 29, pl. 12, fig. 34, pl. 13, figs 17, 18, pl. 14, figs 13, 26 (*Calveria hystrix*); 1927: 282–283, fig. 159 (as *Araeosoma hystrix*); 1935: 222–227, figs 126–128, pl. 23, figs 1–5, pl. 24, fig. 1, pl. 78, fig. 12.

SAMPLES. ES 23(6), ES 178(15), AT 3(3), GT 1(1), GT 7(5), GT 11(4), GT 14(3). [650–805 to 1000 m]

DISTRIBUTION. Throughout the North Atlantic excluding the Norwegian Sea. On the eastern side *Calveriosoma hystrix* is known from south of Iceland down to the Canary Islands; about 180–1800 m; on muddy sand to soft ooze.

The specimens were recovered from hauls between comparatively narrow depth limits on the Hebridean Slope, *C. hystrix* being absent from the numerous hauls taken at greater depths. This may indicate a rather narrow zonation with depth. However, the *Michael Sars* recorded it from 1100–1300 m in the northern Rockall Trough [Greig, 1921 (& 1932)], whilst according to Farran (1913) it 'seems, off the Irish coast, to be a characteristic inhabitant of the ooze between 500 and 700 fathoms' (916–1282 m). This indicates that these limits may vary slightly for different areas.

REMARKS. The colour of the present specimens varied from a pale pink to pale red, the largest measuring 242 mm in diameter after preservation in spirit. The tridentate pedicellariae of this and other large specimens varied slightly from the description of Mortensen (1903, pp. 70–71) who found that the edges of the terminal part of the highly involuted blade of the largest pedicellariae are almost 'straight cut off' and irregularly serrated, and more regularly serrated in pedicellariae of smaller specimens. Here the serrated edges of the terminal part are slightly undulating in profile.

REPRODUCTION. The sexes are separate; the largest oocyte found was in excess of 1250 μm in diameter (Tyler & Gage, 1984*b*), although the general histology of the female appears similar to that of *Phormosoma placenta*.

Hygrosoma petersii (A. Agassiz, 1880)

See: Agassiz, 1881: 76. Mortensen, 1927: 284–285, figs 156, 158, 161; 1935: 202–208, pls 13–17, pl. 18, fig. 2, pl. 19, fig. 2, pl. 78, figs 1, 3–5, 24, 25.

SAMPLES. ES 20(1), ES 129(1), AT 229(2), SWT 18(1), SWT 27(1), OTSB 51301 (?2), GT 17(?3). [1237–2965 m]

DISTRIBUTION. Throughout the North Atlantic; 730–2870 m; on soft ooze.

Although *H. petersii* was first discovered by Alexander Agassiz from *Blake* trawlings off the West Indies and the east coast of North America, it was subsequently found in the eastern North Atlantic from the Azores and off Gibraltar to the Bay of Biscay and off SW. Ireland.

The present records slightly extend the known northward range into the Rockall Trough and the known lower bathymetric limit.

REMARKS. The specimens had lost the majority of their primary spines on the aboral surface; however, sufficient of the characteristically scarcely curved hoofed spines remained to characterise them along with the single rows of tubefeet on the oral side and the deep violet coloured skin that is largely lost by abrasion on trawled specimens, the denuded test being paler coloured.

Both Grassle *et al.* (1975) and Pawson (1982) provide interesting notes on this species from observations from the submersible *Alvin*. Grassle *et al.* diving at 1800 m depth off New England describe *H. petersii* as a 'large, black urchin with long thin spines'. They observed also that *H. petersii* was active, walking about on its ventral spines, the hoof-like tips of which were conspicuously white, so that it was quite difficult to catch using the submarine's mechanical arm. Pawson (1982) remarked that the intestinal contents of specimens collected from the Tongue of the Ocean, Bahamas, consisted almost exclusively of fragments of *Sargassum* and *Thalassia* whilst specimens collected further north appeared to have a more 'mixed' diet. Hence it seems likely that this species is an opportunistic scavenger, like other deep-sea echinothuriids.

REPRODUCTION. Examination of the gonads indicates the sexes to be separate. In the single female examined oocytes up to 1150 μm in diameter were present (Tyler & Gage, 1984*b*).

Sperosoma grimaldii Koehler, 1897

See: Mortensen, 1903: 75–78 pl. 4, figs 3–5, pl. 11, fig. 9, pl. 12, fig. 16, pl. 13, figs 12, 23, pl. 19, figs 2, 4, 4a, 6, 11, 31, 33; 1927: 287–288, fig. 163; 1935: 185–187, figs 107, 108, pl. 8, figs 1, 2.

SAMPLES. ES 99(1), AT 121(3), ES 135(1), AT 221(juvenile, 1), AT 223(1), AT 230(60, ?[juveniles], 23). [1075–2910 m]

DISTRIBUTION. Throughout North Atlantic; 300–2300 m; on soft ooze.

This species was first discovered in trawlings made in the Azores by the Prince of Monaco, its name being taken from the Monagasque royal house. It was subsequently found by the *Michael Sars* in the northern Rockall Trough at 59°28′N, 08°01′W, referred to as the 'Faroe Channel, warm area' by Mortensen (1927), and in the Porcupine Seabight by the *Helga*, recorded by Farran (1913).

REMARKS. The size of the present specimens varies from 120 to 160 mm in diameter which is somewhat less than the maximum 220 mm given by Mortensen (1927). The most abundant catch was in a trawling made on the Hebridean Slope at 1210 m depth.

REPRODUCTION. The sexes are separate; maximum oocyte size observed in female gonads 1100 μm in diameter, but few oocytes were found to exceed 500 μm diameter in the specimens examined (Tyler & Gage, 1984*b*).

Family **PHORMOSOMATIDAE**

Phormosoma placenta Wyville Thomson, 1872

See: Thomson, 1874: 732, pls 62, 63; Agassiz, 1883: 30, pls 12, 13; Mortensen, 1903: 66–70, pl. 4, figs 1–2, pl. 11, figs 7, 10, 25, pl. 12, figs 2–3, 7, 11, 19, 21, 23, 25, 26, 37, 39, pl. 13, fig. 7; 1935: 125–135, pl. 1, figs 1–5, pl. 2, figs 1–19, pl. 74, figs 1–6, 9.

SAMPLES: ES 4(1), ES 20(4), ES 22(4), SBC 67(frag.), AT 68A(juveniles, 2), ES 99(1), ES 105(2), AT 107A(3), AT 161(2), AT 162(140), AT 171(2), AT 177(2), ES 178(4), AT 181(1), AT 186(1), AT 191(juveniles, 10), AT 192(315; juveniles, 1). SWT 10(53), SWT 11(1), SWT 17(134), SWT 18(29), SWT 32(85), AT 3(3), GT 1(3), GT 11(1), GT 14(1), GT 17(5). [650–800 to 2225 m, but see note below]

DISTRIBUTION. North Atlantic from the West Indies to the Davis Strait and from off Iceland and the Faroes south to the Gulf of Guinea in South Atlantic; 260–2484 m; on muddy sand to soft ooze.

We think that the single specimen recorded from a haul at 2500–2560 m (SWT 11) may have been a contaminant from a haul (SWT 10), yielding numerous *P. placenta*, made the previous day in shallower depths nearby. Hence, this record is not taken as an extension of its known vertical range.

This now well-known and easily recognised species was first discovered by Wyville Thomson in dredgings made by the *Porcupine* in the northern Rockall Trough in the year 1869. Mortensen (1903) states that it is essentially a bathyal species 'scarcely occurring in the great depths in the

Atlantic', and indicates that it is probably absent in the 'cold' water areas north of the submarine sills dividing the Norwegian Sea from the North Atlantic. Our records confirm this distributional trend.

Le Danois (1948) regarded *Phormosoma placenta* along with the other echinothuriids, *Calveriosoma hystrix* and *Sperosoma grimaldii,* as characteristic of the faunal association found at 1000–2000 m depth on the NE. Atlantic continental slope.

According to Mortensen (1935), the gut contents include mud pellets, the animal feeding off organic material in the sediment. Pequegnat & Jeffrey (1979) found large numbers of this species in the Gulf of Mexico and western Caribbean to be associated with aggregations of terrestrial vegetation, sea grass and natural tar deposits. Although these authors thought that the plant material was eaten, it is not known whether the hydrocarbon residue is utilised as food.

REMARKS. Grassle *et al.* (1975) observed dense aggregations of this echinothuriid species from the submersible *Alvin* on the bottom at 1300 m depth off New England, although such aggregations of *P. placenta* were not observed by Pawson (1982) from *Alvin* in the Tongue of the Ocean, Bahamas.

REPRODUCTION. Histological examination of the large gonads of specimens from sta. 'M' and elsewhere shows that the sexes are separate and that this species produces large, yolky eggs in excess of 1100 μm in diameter indicative of lecithotrophic or direct development. The gonads are packed with nutritive phagocytic tissue, one type of which appears to provide energy for growth of gametes whilst a second type results from breakdown of relict gametes. There does not appear to be any seasonal cycle in oogenesis indicating that this echinoid probably breeds year-round (Tyler & Gage, 1984*b*).

Order **ECHINOIDA**
Family **ECHINIDAE**
Echinus acutus Lamarck, 1816

See: Mortensen, 1903: 152–159, pl. 1, figs 4, 7–8, pl. 2, figs 1, 2, 6, 8, pl. 15, figs 2, 14–16, pl. 16, figs 2, 5, 10, 16, 18, 22, pl. 18, figs 1, 5–7, 14, 24; 1927: 305–306, figs 144(2), 148(1), 174; 1943: 41–52, pl. 3, fig. 3, pl. 5, figs 1–5, pl. 7, figs 7–9, pl. 8, figs 1–10, pl. 10, figs 1, 2, pl. 54, fig. 26.

SAMPLES. ES 23 (26, ?[juveniles] 5), ES 69(3), AT 223(64), AT 230(5) AT 1(1), AT 3(10), GT 1(2), GT 7(3), GT 14(3), GT 17(5). [750–1210 m)

DISTRIBUTION. North-east Atlantic including the coastal seas around Europe from Bear Island and the Barents Sea south to Cape Bojador, NW. Africa, and the Mediterranean; 20–1280 m; on fine sand to soft mud bottoms.

REMARKS. This well-known and common, morphologically variable, coastal species is known as one of three varieties: *flemingii, mediterraneus* and *norvegicus* each of which was thought originally to be a distinct species.

The present specimens may all be referred to *E. acutus* var. *norvegicus* as defined by Mortensen (1903, 1927, 1943). Although the shape of the test was usually low and slightly conical with a distinctly flattened oral surface, a few specimens were found with a more globular shape. Test and spine colouration, as in previous records, was highly variable. However, pedicellariae were typical of *E. acutus* in all specimens examined. In some cases the spines were an intense scarlet red with whitish tips, and the test a ruddy brown colour, in others the spines were greenish with the test showing a brown or red-brown radial pattern over the aboral side. The maximum size was 79 mm in test diameter which is well within the maximum of ca. 150 mm given by Mortensen (1943).

Although rather modest numbers have been preserved from trawlings from the Hebridean Slope, large numbers of urchins that J.D.G. has identified as this species were collected in Granton otter-trawl hauls from depths between 750–1000 m on fishing cruises of RRS *Challenger* in 1975–1977. Evidently a large population exists at this level on the continental slope. Farran (1913) records *E. acutus* var. *norvegicus* from numerous *Helga* trawlings from around the 500–1200 m depth zone in the Porcupine Seabight. It seems likely that this variety has a ribbon-like distribution on the upper continental slope and submerged banks of the NE. Atlantic. Its bathymetric range overlaps with that of *Spatangus raschi,* both species comprising characteristic elements of the upper slope benthos (Le Danois, 1948).

Observations on the varied gut contents of *E. acutus* are summarised by De Ridder & Lawrence (1982).

REPRODUCTION. Histological study of the gonads of *E. acutus* var. *norvegicus* from the Hebridean Slope indicates a ripening of the ovaries of females in the early spring (Tyler & Gage, 1984*a*). From coastal populations occurring off the south-west of Britain in the first quarter of this century, the breeding season is recorded in the summer months with a well-known and easily recognisable echinopluteus larva. Hybridisation of shallow water specimens of *E. acutus* with *E. esculentus* and *Psammechinus miliaris* has been achieved in the laboratory (Shearer, Morgan & Fuchs, 1914; Hagström & Lønning, 1961*a*) and similar hybridisation is thought to occur in wild populations (Mortensen, 1943; Hagström & Lønning, 1961*b*).

Echinus affinis Mortensen, 1903

See: Mortensen, 1903: 150–152, pl. 5, figs 4, 8, pl. 15, figs 3, 10, pl. 16, figs 6, 10, pl. 18, figs 4, 16, 28, pl. 19, fig. 17, pl. 20, figs 17, 21; 1943; 83–86, pl. 11, figs 1–7, pl. 55, figs 15, 17, 19.

SAMPLES. ES 4(47), ES 12(9), ES 14(1), ES 112(?[juveniles], 1073), AT 114(1), AT 139(4), AT 144(148), AT 151(100), AT 153(180, ?[juveniles] 1), AT 161(?1), AT 167(220), AT 171(222), AT 175(43), ES 176(7, ?[juvenile] 73), AT 177(546), AT 181(615), ES 182(18), ES 184(84), AT 186(486), AT 191(1), AT 195(487), ES 197(110, ?[juveniles]8), AT 198(75), ES 200(62, ?[juveniles]1), AT 201(223), ES 202(1), ES 218(6, ?[juveniles]), AT 219(327), AT 221(1), AT 228(941), SWT 10(282), SWT 13(3), SWT 17(15), SWT 18(182), SWT 32(5). [1605–2450 m]

DISTRIBUTION. Previously known in North Atlantic from south of Iceland, the Denmark Strait, and off the east coast of North America to the Azores; 770–2230 m; on soft ooze.

The present records extend both the lower limit and the known range of this species in the NE. Atlantic.

REMARKS. The maximum size of the specimens was 48 mm in test diameter, which is close to the 51 mm maximum given by Mortensen (1943). The size distribution of samples taken from a repeat station at *c.*2200 m depth where this urchin was abundant was variable, being generally unimodal or sometimes bimodal, with modes from about 26 to 40 mm. The colour of test and spines was generally white with sometimes a slight buff colouration of the musculature of the base of the spines. In some of the shallower specimens (SWT 10, SWT 17 and SWT 18) this was more pronounced as a red/brown colouration imparting a faint radial colour pattern. In small specimens the pink coloured gonads show through the aboral test imparting a faint pinkish hue. Clearly this small, white urchin is abundant at suitable depths in the Rockall Trough. It is probably similarly abundant elsewhere in North Atlantic at suitable depths; Grassle *et al.* (1975) record counts of 259 and 262/100 m^2 from observations from the submersible *Alvin* off New England at around 1800 m depth. It is significant that they saw *Echinus* only once on dives nearby at the shallower depth of 1300 m indicating a bathymetric range of *E. affinis* there probably similar to that for this species in Rockall. A similar bathymetric distribution is indicated by Rowe & Menzies (1969) from bottom photographs taken off the Carolinas. These photographs indicate densities of 0·1–1·0 per photograph (each covering 6·3 m^2) at around 2500 m depth (Rowe, 1971). Haedrich, Rowe & Polloni (1980) record that *E. affinis* ranked fourth and third, respectively, in numerical abundance of megafauna in trawlings at 1384–1947 m and 2116–2481 m off the continental slope south of New England.

Mortensen (1903) remarked that this species had probably been confused with others in sampling prior to the *Ingolf,* notably as *E. norvegicus.* He also remarked that it is closely allied to *E. alexandri* which appears to occur at similar depths. At the northern repeat station, at *c.* 2200 m in the central Rockall Trough east of the Anton Dohrn seamount, *E. alexandri* occurred only rarely. But in a haul from the southern Feni Ridge (ES 112) specimens identified to both *alexandrii* and *affinis* occurred in roughly equal numbers, along with large numbers of small

Echinus (<5 mm) unidentifiable to species with certainty. It was noted that developing gonads were visible in specimens as small as 4 mm in diameter.

Mortensen (1943) noted that the gut of *E. affinis* was full of sediment including foraminiferans. It would appear to be an opportunistic scavenger, apparently actively foraging for phyto-detrital patches (R. S. Lampitt, Institute of Oceanographic Sciences, personal communication) and for larger plant remains which may lead to the formation of small aggregations (Grassle *et al.*, 1975).

REPRODUCTION. As with other members of this genus, the sexes are separate and roughly equal in number. Histological study of the gonad and females from sta. 'M' shows a marked oogenic cycle, ripe oocytes 90 µm in diameter being spawned probably in January/February (Tyler, Grant, Pain & Gage, 1982; Tyler & Gage, 1984*a*). Although early postlarval *Echinus* have been found in bottom hauls taken in May, these, unfortunately, cannot be identified with certainty as *E. affinis*.

Both a growth in size and a decrease in numbers in these postlarvae was evident from comparing samples taken in early June and late September 1973 and similarly from samples taken in late May and mid September 1980. Postlarvae have occurred only rarely in spring or summer samples taken in either year so it appears possible that successful recruitment is variable from year-to-year as occurs in shallow water echinoid populations (see Ebert, 1983 for references). Nothing is known of the age structure of the adult populations, although in view of the variable modal structure it would seem reasonable to suppose that survivorship and longevity is comparable to that in shallow-water populations of *Echinus*.

Echinus alexandri Danielssen & Koren, 1883

See: Mortensen, 1903: 146–149, pl. 5, figs 2, 3, pl. 15, figs 13, 17, pl. 16, fig. 8, pl. 18, figs 9, 11, 19, 23, 25, pl. 19, figs 16, 31, 34, 38, pl. 20, figs 1, 2, 27, pl. 21, figs 18–20, 27; 1927: 304–305, figs 167(1), 172, 173; 1943: 65–68, pl. 11, figs 8–11.

SAMPLES. ES 15(11), ES 20(2), AT 107A(1), ES 112(1), AT 167(1), SWT 18(2). [1271–2300 m]

DISTRIBUTION. North Atlantic from south of Iceland, the Porcupine Seabight, the Bay of Biscay to the Azores, possibly to Tristan da Cunha, and along the east side of North America; 365–3150 m; on soft ooze.

Although not numerous in the Rockall samples, the present records are the first for this species in the Rockall Trough and fall well within its previously recorded bathymetric limits. An overlapping, though slightly shallower distribution in Rockall compared to that for *Echinus affinis* is also indicated from the results of trawlings on the continental slope south of New England (Haedrich *et al.*, 1980).

REMARKS. The maximum size was 51 mm which is a little larger than the maximum for *E. affinis* although in other respects these species appear closely similar. As noted by Mortensen (1903, 1927), *E. alexandri* may be distinguished by its more flattened appearance on the upper side and by its longer spines as well as by differences in pedicellariae figured by Mortensen (1903). A further reliable difference lies in the marked black pigmentation of the tissues around the oral teeth. The light pink colour remarked on by Mortensen (1927) was not noticed in the present specimens, except in young specimens where the developing gonads showed through the thin test, although it is possible that it faded quickly in spirit and was overlooked.

Mortensen (1943) records the gut contents of *E. alexandri* as consisting of bottom mud with foraminiferans.

REPRODUCTION. Preliminary study of the histology of the gonads of *E. alexandri* shows that the sexes are separate with a well-defined oogenic cycle with probable ripening in late winter as with *E. affinis* (Tyler & Gage, 1984*a*). Likewise maximum egg size (100 µm) indicates planktonic development.

Echinus esculentus Linnaeus, 1758

See: Mortensen, 1927: 297–299, fig. 168; 1943: 25–40, pl. 1, figs 1–3, pl. 2, figs 1–4, pl. 3, figs 1–2, pl. 4, figs 6–11, pl. 5, fig. 6, pl. 9, fig. 1, pl. 54, figs 1–7.

SAMPLE. ES 113(1) [168 m]

DISTRIBUTION. North-east Atlantic from the coasts of Finmark and Iceland to Portugal, also known from Lousy Bank; 0–1264 m; on rocky bottoms.

The single, small specimen was taken in a haul from the Rockall Bank. Although reported by the *Ingolf* as deep as 1264 m, *E. esculentus* is uncommon at such depths and usually found only in the shallow waters of the coastline. Hence the new record, while not unexpected on Rockall Bank since it is already known from Lousy Bank, is near its usual lower limit; as Farran (1913) comments 'the occurrence of the common urchin below fifty fathoms seems to be exceptional'.

Echinus elegans Düben & Koren

See: Mortensen, 1903: 142–145 pl. 1, figs 2, 3, pl. 3, fig. 4, pl. 15, fig. 4, pl. 16, figs 3, 19, pl. 18, figs 2, 3, 22, 26, pl. 19, figs 10, 26, pl. 20, figs 8, 9, 19, 22, 23; 1927: 303–304, figs 167, 169; 1943: 61–68, pl. 12, figs 1–8, pl. 13, fig. 1, pl. 14, figs 1–6.

SAMPLES. ES 23(99), AT 230(2), GT 11(9), GT 14(2) [704–1210 m]

DISTRIBUTION. North-east Atlantic from Lofoten and the Trondheimfjord to the Skagerrak, and from south and west of the Shetlands and south of Iceland to the Bay of Biscay, the Azores and the North African coast to Cape Spartel; 50–1710 m; on soft sediment.

REMARKS. This species occurred along with *E. acutus* var. *norvegicus* in ES 23 and AT 230. Specimens ranged from 11 to 66 mm test diameter. The test is usually white with purplish-brown coloured spine musclature and tube feet, although some specimens had a reddish, or occasionally bright green, flush on the apical plates that sometimes continued down the dorsal test between the spines, and was present also on the spines with a white tip.

REPRODUCTION. Mortensen (1943) suggested on the basis of the small-sized eggs that *E. elegans* produced a typical Echinopluteus larva.

Order ***SPATANGOIDA***
Family ***AEROPSIDAE***

Aeropsis rostrata (Wyville Thomson, 1876)

See: Mortensen, 1907: 90–97, pl. 5, figs 8–10, 15, 20, 22, pl. 15, figs 1, 2, 5, 8, 13, 19–21, 29, 37, 40, 43, 52; 1950: 328.

SAMPLES. ES 10(1), ES 56(6), SBC 66(juveniles, 4), SBC 67(?[juvenile] 2), ES 185(1), ES 207(1, juvenile 1). [1200(?1000)–2907 m]

DISTRIBUTION. Previously known from the NW. Atlantic, from the Davis Strait southwards to the deep waters off New Zealand; *c.* 2550–3125 m. Although Agassiz (1881) referred to records of *Aeropsis rostrata* from the Bay of Biscay and coast of Portugal, Mortensen (1907, pp. 93–94) casts doubts on their authenticity. However, the present records indicate that this curious species may be found throughout the North Atlantic at suitable depths.

REMARKS. The largest specimen measured only 8·8 mm in test length compared to the maximum of 34 mm of specimens collected by the *Ingolf* and it seems likely that the present specimens are juveniles. In view of the well-developed fasciole, larger specimens may burrow deeper than the juveniles and hence be missed by the epibenthic sled sampler employed. The two extremely large penicillate tube feet seen in the present specimens, the sucking disk of which Mortensen (1907) notes is the same size in both large (where up to 12 sucking tube feet are developed) and small specimens, indicates a rather specialised function. The function of these large and highly modified tube feet with their webbed discs is unknown (Smith, 1980*a*). It is possible that they assist both in the construction and maintenance of a siphonal tube to the sediment surface, where they may protrude and assist both in feeding and in creating a respiratory current. McCauley & Carey (1967) remarked that the closely related Pacific species *A. fulva* (Agassiz, 1898) 'appears to digest organic material ingested with the sediments because the guts were largely filled with amorphous material, and only a few diatom frustules and sponge spicules could be recognised'.

Family **HEMIASTERIDAE**

Hemiaster expergitus Lovén, 1874

See: Mortensen, 1907: 97–108, pl. 2, figs 1, 4, 18, 20, pl. 4, figs 6–8, 10–12, pl. 15, figs 9, 16–18; 1927: 323–324, figs 186, 187; 1950: 387–389.

SAMPLES. ES 4(9), ES 27(juvenile, 1), SBC 58(1), SBC 63(juvenile, 1), SBC 66(postlarvae 4), SBC 68(1), ES 105(1), ES 118(juvenile, 1), ES 129(1), ES 137(1), ES 143(1), AT 144(1), AT 181(2), ES 184(juvenile, 1), AT 186(2), ES 190(2), ES 200(? 1, (juvenile) 1), ES 202(1, ?[juvenile], 2), ES 204(?[juvenile], 1), SBC 205(postlarva, 1), SBC 216(1), AT 219(9), AT 221(4). [1200–2910 m]

DISTRIBUTION. Previously known throughout the North Atlantic from south of Iceland and the Davis Strait to the West Indies and in the east, the Porcupine Seabight and the Azores and Cape Verde Islands; 950–3200 m; burrowing in soft ooze.

The present records fall within the known bathymetric range although they extend the geographical range to the Rockall Trough. Mortensen (1927) casts doubts on the authenticity of the *Michael Sars* record in 1902 from 61°40′N, 03°11′E (400 m depth, temperature 6·34°C) north of the Viking Bank in the northern North Sea.

REMARKS. The largest specimen measured 32 mm in length and was recovered from a box core sample (SBC 216) where it was discovered lying in its burrow 12 cm from the surface of the sediment. A long, slightly oblique, siphonal burrow could be traced linking it to a shallow depression and opening in the sediment.

Analogies on functional morphology may be drawn from the results of the detailed studies on the shallow-water amphisternate spatangoids, *Echinocardium* and *Moira* (Nichols, 1959; Chesher, 1963; Péquignat, 1970). The large sucker-like disk and highly extensile stem of the conspicuous, brown-coloured tube feet of that part of the anterior ambulacrum lying within the roughly oval mucus-secreting peripetalous fasciole probably have a feeding function. They may also be used to construct and maintain the siphonal tube, the full length of which they are probably capable of extending. Certainly, the width and size of the peripetalous fasciole suggests a capability for generating a strong current while the opening of the funnel in the bottom of a shallow depression may serve as a trap for particles carried along by currents over the sediment surface.

Family **SPATANGIDAE**

Spatangus raschi Lovén, 1869

See: Mortensen, 1907: 129–132, pl. 1, figs 4, 5, pl. 2, fig. 19, pl. 16, figs 17, 23, 28; 1927: 329–330, figs 192, 193; 1951: 14–15.

SAMPLES. ES 23(6), AT 132(1), GT 7(1), GT 14(2). [225–761 m]

DISTRIBUTION. From the Norwegian coast off Tromsø, Porcupine Seabight, Bay of Biscay to Gibraltar, also west and south of Iceland; 150–1500 m; on muddy bottoms.

The present records are from the upper Hebridean Slope except for AT 132 which was a haul on the Porcupine Bank. Large numbers of this species were obtained at depths from 146 m to 1024 m in the Porcupine Seabight and Porcupine Bank areas by the *Helga* (Farran, 1913). The numbers recorded above do not reflect the abundance of this urchin caught in the Granton otter trawl hauls made at around the 700 m level on the Hebridean Slope. Evidently a large population exists, along with *Echinus acutus* var. *norvegicus*, at about this depth. It is likely that both urchins have a ribbon-like zonation along the upper continental slope and outer banks lying to the west of the British Isles. The distribution of *S. raschi* overlaps that of the somewhat deeper range of *E. acutus* var. *norvegicus* (Le Danois, 1948).

REMARKS. Nichols (1959) gives some information on the semi-buried ploughing movement of this species from aquarium observations.

Brissopsis sp.

SAMPLES. ES 99(1). [1160 m]

REMARKS. This specimen was fragmented but could clearly be referred to this genus, the apical system possessing four clearly defined genital pores within the typical *Brissopsis* peripetalous fasciole. The test was delicate and pale fawn/white in colour with the fasciole showing up brown. The arrangement of the plates of the anterior ambulacrum outside the petal quite closely resembles the arrangement given by Mortensen (1951, p. 383, fig. 184) for *B. lyrifera*.

Pedicellariae were also recovered (Fig. 3), the single globiferous pedicellaria found agreeing somewhat with Mortensen's (1907) description of *Brissopsis alta* in possessing multiple teeth, some minutely bifurcate at the tip. The remaining pedicellariae were all tridentates, and although large (up to 1·75 mm blade length) were broadly tapering with minute teeth and probably similar to the third type of tridentate that Mortensen described for *B. lyrifera* (1951, pl. 19, fig. 10).

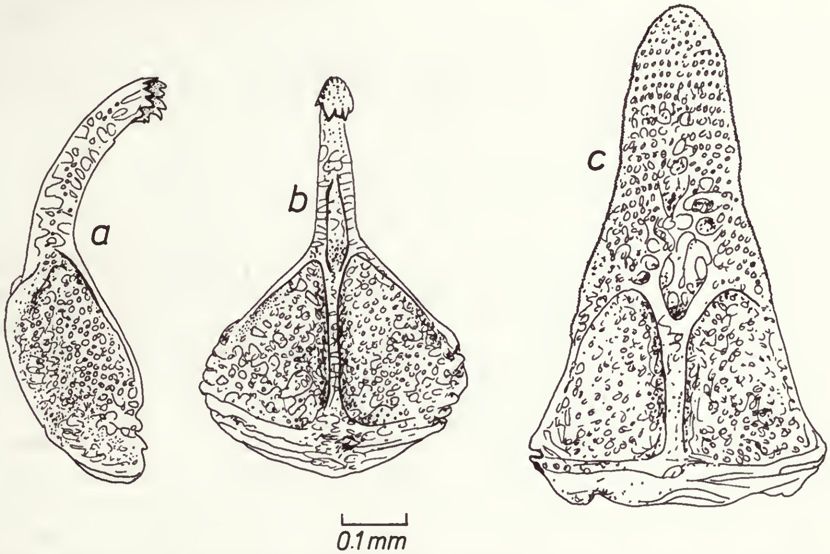

Fig. 3 *Brissopsis* sp. from ES 99: lateral (a) and inside (b) views of globiferous and tridentate (c) pedicellariae.

Brissopsis sp.

SAMPLE. ES 22 (fragments of several + 12 entire juveniles). [1028 m]

It is uncertain whether these specimens represent the same species as the previous *Brissopsis* sp., although in view of the similar depth this seems quite possible. The juveniles measured from 1·1 to 4·2 mm in test length.

Order **POURTALESIOIDA**
Family **POURTALESIIDAE**

Pourtalesia miranda A. Agassiz, 1869

See: Mortensen, 1907: 63–68, pl. 5, figs 1–7, 11, 12, pl. 8, figs 1–3, 7, pl. 11, figs 1, 13–14, 18–20, 23, 34–37, 40–41; 1927: 346, fig. 207 (both as *P. wandeli*); 1950: 144–145.
[We follow Clark (1914) in regarding *P. wandeli* Mortensen, 1905 as conspecific with the West Indian type of *P. miranda*; see below.]

SAMPLES. ES 2(1), ES 6(41), ES 111(1), ES 118(1), ES 169(?[juvenile] 1), ES 176(1), ES 180(3), ES 185(7), ES 190(14), ES 204(56, ?[juvenile] 1), ES 207(5). [2245–2910 m]

DISTRIBUTION. Throughout the North Atlantic, from the West Indies to the Davis Strait and south of Iceland to the Bay of Biscay; 450–5850 m; in soft ooze.

Evidently, *P. miranda* is restricted to the greatest depths in the Rockall Trough, consistent with its limitation to abyssal depths, at least in the NE. Atlantic.

REMARKS. There has been considerable confusion over whether or not *P. miranda* and *P. wandeli* are conspecific, due to our lack of knowledge of the extent of variation. David (in press) describes the development of the plates and the size-related changes in shape of *Pourtalesia miranda*. Clark (1914) considered the two to be synonymous having compared specimens from western Greenland, identified as *P. wandeli* by Mortensen (1907), and from Grenada identified as *P. miranda* by Agassiz himself. Mortensen (1950) had considerable doubts about the synonymy, but maintained it concluding that 'Until a critical examination of the rich material of *Pourtalesia* from the West Indies has shown definitely that it is all only one species, I must reserve my doubts as to the identity of the said species'.

The largest of the present specimens measured 21·8 mm in length. This is considerably less than the maximum of 53 mm found in the *Ingolf* samples, although there is close agreement with the plate structure figured by Mortensen (1907). However, of the 122 specimens recovered by the *Atlantis* off Cuba, the largest measured only 25 mm long (Clark, 1941). Fig. 4 shows that slight differences in the shape and proportional size of the anal snout seen in the present specimens may be arranged in an ontogenetic series that grades into the two large specimens figured by Mortensen (1907).

Postlarvae of pourtalesiid species occurred quite often in the epibenthic sled hauls, but only sizes > *c.* 3 mm could be distinguished from those of *Echinosigra*. Mironov (1975) has on the basis of test and spine morphology inferred that the Pourtalesiidae burrow in soft sediment. The presence of the spatulate spines on the upper, aboral side of the test in *Echinosigra* and some *Pourtalesia* was taken as evidence of their ability to burrow completely into the sediment. However, Smith (1980*a,b*) noted that there may be some doubt as to whether *Pourtalesia* is normally a burrowing species since sea-bed photographs taken both in the southern Bay of Biscay (Southward *et al.*, 1976) and off NW. Africa (Rice *et al.*, 1979) clearly shows specimens moving *over* the sediment, using their spines. Smith (1980*b*) infers from their gut contents that species of this genus are sediment swallowers, and that they probably feed by ploughing forward through the sediments, funnelling the surface layer of sediment into the frontal recess.

REPRODUCTION. The sexes are separate; in females vitellogenic oocytes ranged from 90 to *c.* 300 μm in greatest dimension; ripe eggs were filled with yoke indicating lecithotrophic development. Oocyte-size frequencies showed no significant differences between samples taken in January, April and May. Potential fecundity is around 3800 oocytes per individual but evidence of internal degeneration of oocytes suggests that actual fecundity will be less (Harvey & Gage, 1984).

Pourtalesia jeffreysi Wyville Thomson, 1873

See: Mortensen, 1907: 58–63, pl. 5, figs 13–14, 16–19, 21, 23, pl. 7, figs 2–4, 11, 12, 14, 21, pl. 8, figs 4–6, 8–11, pl. 11, figs 4, 7–10, 30.

SAMPLE. AT 90A(3). [1040 m]

DISTRIBUTION. Norwegian Sea and Kara Sea area of the Arctic Ocean, Baffin Bay; 50–3016 m; mud bottoms. The present specimens were recovered from a haul from the southern part of the Faroe/Shetland Channel, on the northern flank of the Wyville Thomson Ridge and a little south of the type locality, *Porcupine* station 64.

REMARKS. The specimens measured 30, 31 and 36 mm in length with well defined genital pores visible in all three. Large collections of this species were obtained by the *Jean Charcot* on the NORBI expedition in 1975; on the basis of a biometrical analysis of test variation David (1983) has shown morphological differences in those from different basins in the Norwegian Sea. These differences are interpreted as an early stage in speciation as a result of geographic isolation.

Specimens of the leptonacean bivalve *Montacuta (Axinodon) symmetros* (Jeffreys, 1877) were found attached by a byssus to spines of the NORBI *P. jeffreysi* (Dr A. Warén, University of Gothenburg, personal communication). There is probably a similar association of *Montacuta symmetros* with the *Pourtalesia* in the Bay of Biscay (Dr Eve Southward, Marine Biological Association, Plymouth, personal communication and observations by J.D.G. from specimens collected by the *Jean Charcot* in the northern Bay of Biscay in 1976, INCAL cruise). Furthermore, Mironov (1978) notes unidentified montacutid bivalves attached to the ventral spines of *Pourtalesia heptneri* from the Banda Trench. There is, unfortunately, still only indirect evidence that a similar association is developed in the Rockall Trough, *Montacuta symmetros* having been found in sievings of the same hauls where *Pourtalesia* and *Echinosigra* were taken. It also remains unknown whether *M. symmetros* is restricted to one or the other species, or whether it forms an association with both.

Reproduction. The sexes are separate; one of the 4 gonads present in the single female collected contained only five ripe ova averaging 225 µm in diameter, their size and yolky appearance suggesting lecithotrophic development of the larva (Harvey & Gage, 1984).

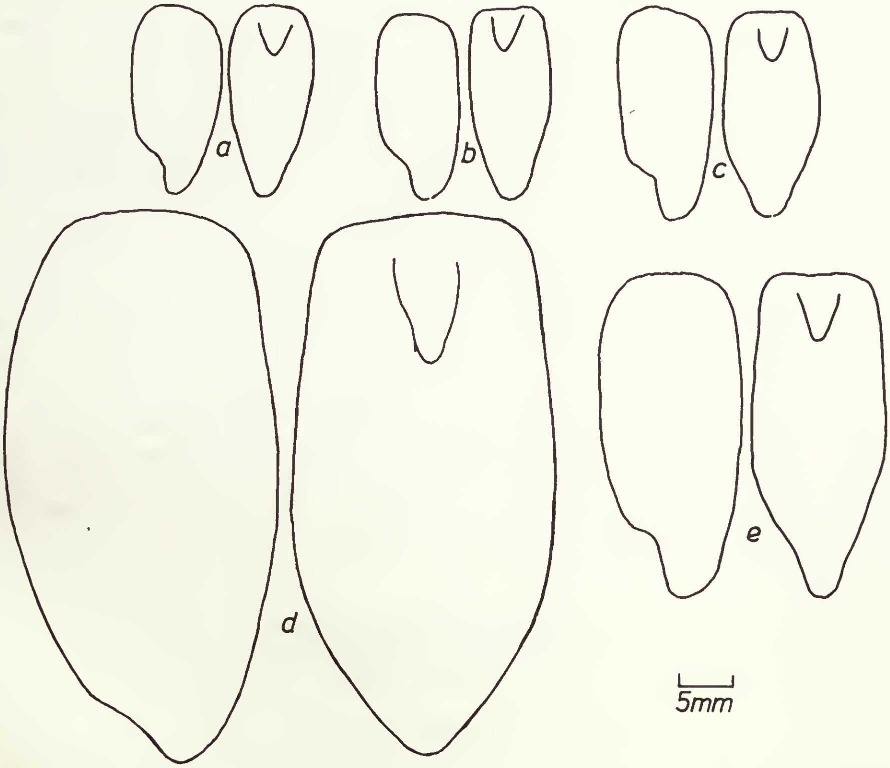

Fig. 4 Lateral and central views of tests of *Pourtalesia miranda*. a–c, present specimens from the Rockall Trough; d and e, re-drawn to scale from Mortensen (1907, pl. 5, figs 2, 6, 11, 12).

Echinosigra phiale (Wyville Thomson, 1874)

See: Mortensen, 1907, 68–72, pl. 6, figs 1, 2, 7, pl. 7, 1, 7, (as *E. phiale*); 72–77, pl. 6, figs 3–6, 17–21, pl. 7, figs 5, 10, 16, 18, pl. 11, figs 2, 3, 5, 6, 17, 21, 24, 25, 27–29, 32, 42–44 (as *E. paradoxa*); 1950: 152–153, 1532 (as *E. paradoxa*).

SAMPLES. ES 4(1), ES 6(35), ES 27(5), ES 56(3), ES 57(1), SBC 58(1), ES 59(1), ES 112(2), ES 118(5), AT 121(13), ES 129(5), ES 135(3), ES 137(5), ES 140(7), AT 141(3), ES 143(2), ES 147(?(juvenile) 2), ES 152(3), AT 154(2), ES 164(3), AT 171(3), SBC 174(1), ES 176(5), ES 180(4), ES 185(31), ES 190(16), ES 197(3), ES 200(1), FS 204(2), SBC 205(3), ES 207(4). [1993–2912 m]

DISTRIBUTION. South and south-west of Iceland and the Rockall Trough; 1540–2377 m; soft ooze. [Mironov (1974*a*) refers both the *Challenger* Expedition record (Agassiz, 1881) and Mortensen's (1909) record of *E. (Pourtalesia) phiale,* both from the Southern Ocean, to the species *E. amphora* Mironov, 1974.] The present records extend the lower depth limit of *E. phiale* in the Rockall Trough.

REMARKS. On the basis of examination of the abundant material occurring in the present samples, Gage (1984*a*) has confirmed Mironov's (1974*b*) synonymy of *E. paradoxa* (Mortensen, 1905) with *E. phiale* on the basis of the original descriptions, by showing that the relatively larger specimens which Mortensen (1907) named *E. paradoxa* represent the adult form of *E. phiale* (Wyville Thomson) which was discovered originally in a *Porcupine* dredging from the Rockall Trough (56°44'N, 12°52'W, 2221 m) as juveniles. The types represent the early stages of growth before elongation to the extraordinary form of the adult. The test is differentiated into head, neck, body and tail, with usually only the head and neck being found intact in trawl hauls. Although early postlarvae could not with confidence be separated from early stages of *Pourtalesia miranda,* the elongated form and neck-like constriction in the test of stages >3 mm could be easily distinguished as *E. phiale*. Gage (1984) traces an allometric series in growth from the *phiale* to the *paradoxa* stages. The largest entire specimen measured 51·8 mm in length whilst similar or larger sizes could be inferred from the many head-end fragments, a clear allometric relationship being established between the width of the head and total length (Gage, 1984*a*).

Mironov (1975) has speculated on the mode of burrowing of this and other pourtalesiid species. The urchin is thought to lie with a horizontal posture in a shallow burrow connected to the sediment surface by means of a short funnel above the apical system. The conspicuous circumferential fasciole on the 'tail' is thought to facilitate the removal of fine sediment and water from the burrow and produce an inward flow through the burrow entrance. Since this burrow entrance would be maintained by the activity of the tuft of spine on the aboral surface of the head, Mironov (1975) concluded that the length of these spines would determine the depth of burrowing as roughly half the height of the test.

REPRODUCTION. The sexes are separate. Gonads develop in individuals above 21 mm in length. Ripe ova were found in samples from March, April, August and November and varied from 250 to 335 µm in diameter, showing no apparent correlation with body size. Their yolky appearance suggests lecithotrophic or direct development of the larva. Size-frequency histograms for oocytes show a range of sizes, including ripe oocytes, being present throughout the year, indicating semi-continuous, year-round reproduction (Harvey & Gage, 1984).

Class **HOLOTHURIOIDEA**
Order **DENDROCHIROTIDA**
Family **PSOLIDAE**

Psolus pourtalesii Théel, 1886

See: Théel, 1886*b*: 14–15, fig. 6; Deichmann, 1930: 188–189, pl 20, figs 5–7; Heding, 1942: 36, figs 39–40, pl. 1, figs 1–2.

SAMPLE. AT 191(3). [2190 m]

DISTRIBUTION. South and SE. of Iceland, Rockall Trough, Labrador Sea, off New England and the West Indies; 1096–2271 m.

REMARKS. The present specimens measured *c.* 30 mm in length and were attached to a large boulder. It is probable that, like its congeners, *P. pourtalesii* is a suspension feeder. The presence of this holothurian on the Feni Ridge, together with a number of suspension-feeding ophiuroids

(Gage *et al.*, 1983) probably results from the high current activity in this area (Ellett & Roberts, 1973).

Psolus squamatus (Koren, 1844)

See: Mortensen, 1927: 417–419, figs 253, 254; Imoaka, 1980: 361–371, figs 1–9.

SAMPLES. GT 1(2, juveniles, 2). [713 m]

DISTRIBUTION. North-east Atlantic from SW. Ireland to the Lofoten Islands, NW. Atlantic, around the southern part of South America including the Falkland Islands, off South Africa, along the eastern border of the Pacific and off Japan; 7–1087 m. This species seems to be more common in higher latitudes.

REMARKS. The wide separation of localities has led to some uncertainty as to whether all the records could be referred to the same species. Ekman (1925) proposed that a southern form could be distinguished, but more recently Pawson (1969) and Imoaka (1980), using material taken off Chile and Japan respectively, have proposed that all the records should be referred to the same species.

P. squamatus is a suspension-feeding holothurian and is commonly found on stones and boulders. The feeding mechanism for the related species *P. chitinoides* has been described by Fankboner (1978).

Family **CUCUMARIIDAE**

Abyssocucumis abyssorum (Théel, 1886)

See: Théel, 1886*a*: 66–69, pl. 4, figs 6–7, pl. 5, fig. 1, pl. 16, fig. 6; Heding, 1942: 33–35, figs 34–36; Cherbonnier, 1941: 93–96, figs 1, 3: j, n–p.

SAMPLE. SWT 15(1). [4810 m]

DISTRIBUTION. Cosmopolitan; 869–4636 m. Ekman (1927) referred to a juvenile specimen from 385 m in the Antarctic but Hansen (1975) believed that it may have been misidentified. The bathymetric limits include the records of *Cucumaria sluiteri* (Ohshima, 1915) which Heding (1942) considered to be synonymous with *Abyssocucumis abyssorum*. The present record slightly extends the known lower bathymetric limit.

REMARKS. This specimen (100 mm long) is the largest recorded in the North Atlantic although several others of a similar size were taken by the *Challenger* Expedition in the south Pacific (Théel, 1886*a*). The posterior end is caudiform but unlike Théel's description the skin is fairly thick and possesses many spicules. The specimen is yellowish-white in colour with numerous small light brown pigment spots distributed all over the surface, as originally described by Marenzeller (1893). The tube-feet are more abundant than drawn for the type specimen, there being about 36 in number arranged in an irregular double row along each ambulacrum. Comparison with the specimens taken by the *Challenger* Expedition indicates that such a high number is not unusual. The body-wall deposits are mainly four armed crosses lacking a spire but with one arm disproportionately developed. This arm, which protrudes obliquely from under the skin, is very spinous at its end and has several small tooth-like spines on the stem. Heding (1942) noted that this type of deposit is more common in large specimens.

Order **DACTYLOCHIROTIDA**
Family **YPSILOTHURIIDAE**

Ypsilothuria talismani talismani E. Perrier, 1886

See: Heding, 1942: 26–27, text-figs 24, 25 figs 5, 6, text-fig. 26 figs 1, 3, text-fig. 27 fig. 3, text-fig. 28 figs 1, 2, text-fig. 29, pl. 2, figs 13–16, 21–30.

SAMPLES. ES 20(7), ES 22(3), SBC 67(4), SBC 69(juveniles, 2), ES 99(3). [*c*. 1000–1271]

DISTRIBUTION. North-east Atlantic; 557–2018 m. The present records support Heding's (1942) suggestion that *Y. talismani talismani* is an upper slope species rarely occurring deeper than 1500 m. Heding (1942) erected another subspecies, *Y. talismani elegans*, for a specimen taken in the West Indies.

REMARKS. For taxonomic details see the description of *Y. bitentaculata attenuata*. The feeding strategy of *Ypsilothuria* is unknown. The curious tentacle arrangement in which the two lateral tentacles on opposite sides are capable of considerable elongation, probably reflects the surface deposit feeding activities of this essentially sedentary species. The closely related genus *Echinocucumis*, which is similar in its body shape and in having larger lateral tentacles, lives buried in mud with only the mouth and anal prolongations above the sediment (Mortensen, 1927):

Ypsilothuria bitentaculata attenuata R. Perrier 1902

See: Heding, 1942: 28–29, text-figs 24, 25 figs 1–4, text-fig. 26 figs 5–7, text-fig. 27 fig. 5, text-fig. 30 figs 1, 2, pl. 2, figs 1–2, 5–10.

SAMPLES. ES 4(28), ES 6(266), ES 8(1), ES 10(20), ES 12(4), ES 27(38, juvenile, 1), ES 34(juvenile 1), ES 52(1), ES 54(1), ES 55(10), ES 56(4), ES 57(2), ES 59(9), ES 111(8), ES 118(19), AT 119(19), AT 121(49), ES 122(12), ES 129(1), AT 130(1), ES 137(19), ES 140(32), AT 141(28), ES 143(3), AT 144(108), ES 147(21), SBC 150(1), AT 151(78), ES 152(117, juveniles 25), AT 153(239), AT 154(73), ES 164(35, juveniles 9), ES 169(8, juveniles 1), AT 171(157), ES 172(10, juveniles 21), AT 175(17), ES 176(44, juveniles, 13), AT 177(381), ES 180(17, juveniles 9), AT 181(75), ES 184(19, juveniles 15), ES 185(153), AT 186(12), ES 190(45), AT 191(7), AT 192(1), AT 195(134), ES 197(329), AT 198(1), ES 200(105), AT 201(10), ES 202(25, juveniles 13), ES 204(78, juveniles 3), ES 207(73, juveniles 3), AT 219(38). [*c.* 1862–2951 m]

DISTRIBUTION. North Atlantic from Davis Strait to West Africa. 1836–3231 m. Heding (1942) considered the North Atlantic specimens to be a variety of *Y. bitentaculata*. This species probably has a cosmopolitan distribution and is common in the Pacific between 250 and 4000 m (Pawson, 1965). Heding (1942) considered *Y. bitentaculata attenuata* to be a lower slope species found at depths greater than 1800 m.

REMARKS. Heding (1942) distinguished *Y. bitentaculata attenuata* from *Y. talismani talismani* on the basis of the shape and size of the calcareous plates, the shape of the deposits in the two large tentacles, and by the shape of the lateral interradial plates of the calcareous ring. A comparison of specimens of a similar size of the two species shows that the body-wall deposits of *Y. bitentaculata attenuata* are consistently larger than those of *Y. talismani talismani* although the difference in size noted by Heding (1942) may occur only in the largest specimens. The development of the deposits in the large lateral tentacles is also related to the size of the specimen (J.D.G. unpublished data). The shape of the lateral interradial plate of the calcareous ring is the most consistent taxonomic characteristic between the two species. In *Y. talismani* the plate has a tooth-shaped anterior process ending in a sharp point, while in *Y. bitentaculata attenuata* the anterior process is usually bifurcate, although in some cases it may have a simple blunt end. In all cases the anterior process is broader than in *Y. talismani talismani.* It should be noted that Heding (1942) refers erroneously to lateral radial plates on page 26, and the plates figured in text-fig. 26 are the lateral interradial and latero-ventral radial. The mid-ventral radial is only present in Figs 4 and 8.

Heding (1942) considered that differences in the body-wall deposit size and structure, and in the shape of the calcareous ring plates were sufficient to refer *Y. attenuata* as a subspecies of *Y. bitentaculata*. The North Atlantic specimens may be found in future to fall within the total variation expected for *Y. bitentaculata*.

In all of the specimens examined the gut was filled with sediment indicating a deposit-feeding mode of life as described for *Y. talismani talismani.* The large variation in the number of specimens taken between hauls probably indicates a patchy distribution.

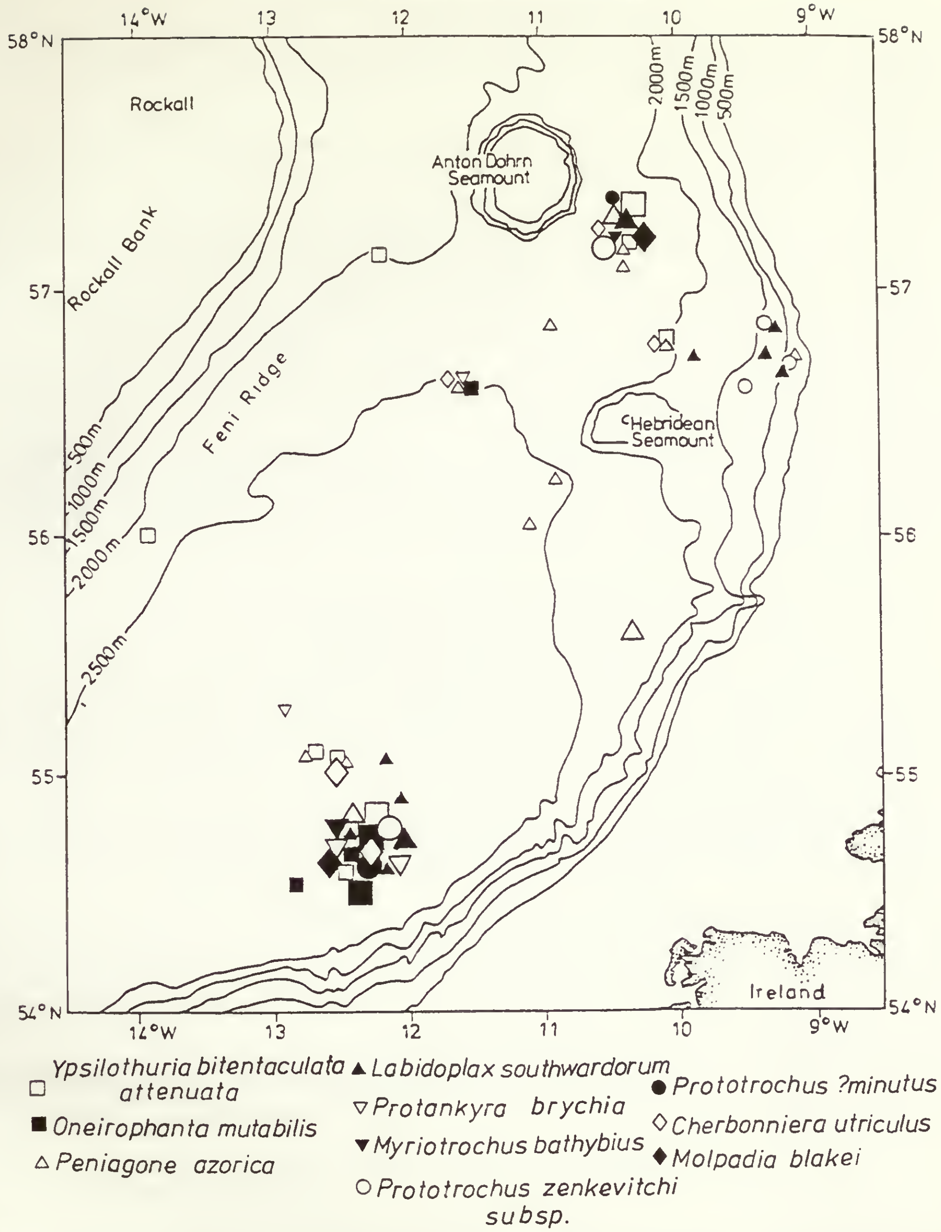
14°W
13
12
11
10
9°W
58°N
57
56
55
54°N
Rockall
Rockall Bank
Feni Ridge
Anton Dohrn Seamount
Hebridean Seamount
Ireland
500m
1000m
1500m
2000m
2500m
□ Ypsilothuria bitentaculata attenuata
■ Oneirophanta mutabilis
△ Peniagone azorica
▲ Labidoplax southwardorum
▽ Protankyra brychia
▼ Myriotrochus bathybius
○ Prototrochus zenkevitchi subsp.
● Prototrochus ?minutus
◇ Cherbonniera utriculus
◆ Molpadia blakei

Fig. 5 Chart of central part of Rockall Trough showing station locations for records of the ten most abundant holothurian species.

Reproduction. The reproductive biology of *Y. bitentaculata attenuata* was studied by Tyler & Gage (1983) under the name of *Y. talismani*. The sexes are separate. The tubules of the gonad ramify throughout the dorsal body cavity close to the gut. In females, oocyte development is synchronous within, but asynchronous between, individual tubules. Study of a time series of samples provides no evidence for annual periodicity in development of the gonads of both sexes. Oocytes grow to a maximum of 350 μm in diameter. This, together with a maximum fecundity of up to 50 oocytes per individual, is interpreted by Tyler & Gage (1983) as indicative of an 'abbreviated', probably lecithotrophic, larval development.

Echinocucumis hispida (Barrett, 1857)

See: Mortensen, 1927: 404–405, figs 242, 243; Pawson, 1965: 8–10, text-fig. 1 fig. 1, text-fig. 2.

SAMPLE. SBC 67(4). [*c.* 1000 m]

DISTRIBUTION. North-east Atlantic, West Indies and east of New Zealand, probably cosmopolitan; 50–1400 m.

REMARKS. The specimens were obtained from the washings of a sandy mud sediment obtained by the 0·25 m^2 box corer on the Hebridean Slope. Four specimens of *Ypsilothuria talismani talismani* also occurred in this sample. Although possessing a similar body morphology, they may easily be distinguished by differences in the calcareous plates of the body wall. The plate of *Ypsilothuria* has a thick stereom with small holes and may be made up of several layers, particularly around the centre where the spire is found. The spire is usually a complex structure made up of many fused pieces. The plate of *Echinocucumis* has much larger holes and the spire, which is placed to one side, is made up of only a few fused pieces.

The co-occurrence of *Y. talismani* and *E. hispida* in this sample indicates an overlapping vertical range. Mortensen (1927) describes *Echinocucumis hispida* as living buried in the mud, with only the mouth and anal prolongation of the U-shaped body projecting above the sediment.

Order **ASPIDOCHIROTIDA**
Family **SYNALLACTIDAE**

Bathyplotes natans (M. Sars, 1868)

See: Mortensen, 1927: 384–385, figs 228: 2, 229; Heding, 1942: 10–12, figs 10–11, 12: 1–2; Pawson, 1965: 16–18, fig. 4.

SAMPLES. GT 17(3). [1237 m]

DISTRIBUTION. Essentially cosmopolitan; about 200 to 1600 m. In the NE. Atlantic *B. natans* usually occurs between 600 and 1600 m, rising to about 200 m off Norway.

REMARKS. The specimens were in poor condition. They were orange in colour and devoid of spicules except in the papillae on which the identification is based. Wesenberg-Lund (1941) recorded a commensal polychaete, *Harmothoë bathydomus* Ditlevsen, 1917, on *B. natans* but it was not present on these specimens. *B. natans* has long been known to be able to swim by undulating its body (Sars, 1868), hence the specific name.

REPRODUCTION. Mortensen (1927) noted that the sexes are separate and that the large, yolky eggs probably indicate direct development.

Benthothuria funebris R. Perrier, 1902

See: Perrier, 1902: 365–371; Heding, 1940: 363–364; 1942: 6.

SAMPLES. ES 27(1), ES 28(?juvenile 1), AT 119(1), AT 121(1), ES 147(3), ES 152(2), ES 169(1), SWT 12(1), SWT 27(1), OTSB 51001(2), OTSB 51301(7). [2890–2996 m]

DISTRIBUTION. Off NW. Africa and SW. Greenland; 782–2700 m.

The samples taken extend the lower bathymetric limit to 2996 m, and provide a geographic link between the previous records. It appears that this holothurian occurs deeper in more northerly latitudes (2700–2996) than off NW. Africa (782–1230 m). If *B. funebris* is synonymous with *B. valdiviae* Heding, 1940 (see below) then the lower bathymetric limit is 4636 m and the species extends to the Indian Ocean.

It may appear from the present samples that *B. funebris* is not a particularly common holothurian. However, this is probably due to a patchy distribution as 67 specimens were taken in one haul by an IOS trawl at the same locality as these records (D.S.M.B. unpublished data, St. 50701, 11 Oct. 1979, 2870–2890 m; 54°34′N, 11°54′W).

REMARKS. Although *Benthothuria* may be sampled in good condition the gelatinous dorsal surface is notoriously difficult to preserve, leading to difficulties in identification. Heding (1940) proposed five species for the genus *Benthothuria,* although he questioned the validity of *B. cristatus* and considered *B. funebris* to be synonymous with *B. valdiviae*. These latter two nominal species differed in two respects; the number of polian vesicles and the presence or absence of large papillae along the dorsal ambulacra. Like the *Ingolf* specimen (Heding, 1942) the Rockall specimens possess two polian vesicles, which is at variance with the single polian vesicle found in the type specimen of *B. funebris*. However, two specimens of *Benthothuria* sampled off NW. Africa (14°50·8'N, 17°50·6'W, 1430 m) in an area not far from the type locality, both also possessed two polian vesicles (D.S.M.B., unpublished data). These specimens resembled *B. funebris* in all other respects although they were larger; however, their poor state of preservation did not permit the presence of large dorsal papillae to be ascertained. Like *B. valdiviae* the Rockall specimens possess some larger papillae along the dorsal ambulacra in addition to the small papillae that are scattered over the dorsal surface, particularly in the lateral interambulacra. The large dorsal papillae are usually retracted and are exceedingly difficult to distinguish in poorly preserved specimens. Heding's proposal that *B. funebris* and *B. valdiviae* are conspecific would appear to be correct, but the matter still awaits the comparison of well-preserved specimens from the type localities. Heding's (1940) classification placing the genera *Benthothuria, Paroriza* and *Pseudostichopus* within the family Gephyrothuriidae under the order Aspidochirotacea has been rejected by most specialists. Deichmann's (1940) classification placing the Gephyrothuriidae, with the single genus *Gephyrothuria,* within the Molpadiida, and placing the genera *Benthothuria, Paroriza* and *Pseudostichopus* within the Synallactidae is generally adopted. In our view, *Benthothuria* is undoubtedly a synallactid with many features in common with *Paelopatides*.

The specimens are white dorsally and purple ventrally; although fairly robust when they first reach the deck the dorsal surface soon starts to break down into a gelatinous mass. They appear to be neutrally buoyant. *B. funebris* may attain a considerable size and the dorsal surface appears to increase disproportionately in mass to the length of the animal during growth. As with *Paelopatides grisea,* the body cavity of the holothurian is less than one-third of the total body volume. Deep-sea photographs of *Benthothuria* can be found in Heezen & Hollister (1971, p. 85) and Pequegnat *et al.* (1972, pp. 90, 95).

Paelopatides grisea R. Perrier, 1902

See: R. Perrier, 1902: 361–365.

SAMPLE. AT 161(3). [2055 m]

DISTRIBUTION. North-east Atlantic, 1918–4060 m, record confirms that *P. grisea* occurs generally at depths of about 2000 m. It is common at these depths in the Porcupine Seabight (D.S.M.B., unpublished data) and in the Bay of Biscay (Sibuet, 1977—recorded as *P. gigantea*).

REMARKS. The species of *Paelopatides* are sometimes difficult to distinguish owing to the damage that the gelatinous body sustains during sampling and preservation. Although Deichmann (1930) considered *P. grisea* to be synonymous with the NW. Atlantic species *P. gigantea* (Verrill, 1884), Heding (1940) believed that the two could be separated depending on the number of polian vesicles. Like the type of *P. grisea,* the present specimens possess two polian vesicles, one of which is large while the other is of variable size but generally small. Since the number of vesicles is the only known difference between *P. grisea* and *P. gigantea* and is a character of doubtful taxonomic significance, the NE. and NW. Atlantic forms of the holothurian may prove not to be specifically distinct when a thorough comparison can be made.

Paelopatides is almost neutrally buoyant and has been observed from submersibles to swim by undulating its body (Grassle *et al.,* 1975; Pawson, 1976). A bottom photograph, taken using a combined trawl and forward-looking deep-sea camera system, clearly shows a large *Paelopatides* >40 cm long from 1942–1949 m depth off the NW. African coast (Rice *et al.,* 1979). It is interesting that these authors note that this specimen was not recovered in the trawl catch. This holothurian also appears to have a rather patchy distribution (Sibuet, 1977; Pawson, 1982).

Despite its gelatinous body, the organic composition of its body wall is remarkably similar to that of other deep-sea and shallow-water holothurians (Sibuet & Lawrence, 1981).

REPRODUCTION. Eggs grow to a size in excess of 1200 µm (P.A.T. unpublished data).

Mesothuria cathedralis Heding, 1940

See: Heding, 1940: 336–338. fig. 5; 1942: 8–9, fig. 8.

SAMPLE. ES 10(1). [2540 m]

DISTRIBUTION. Previously known only from the Gulf of Guinea, from off Cape Bojador and in the Irminger Basin off southern Greenland; 2137–2480 m. The present record increases the lower bathymetric limit to 2540 m and provides a geographic link between these discontinuous localities in the North Atlantic.

REMARKS. The specimen is small (23 mm long) with tube-feet all over the body, small ventrally and larger laterally. The spicules are tables generally with 8 holes in the base and with a tall spire ending in four points which are almost smooth and not as thorny as figured by Heding (1940). Reduced tables are found in the tube-feet.

Mesothuria lactea (Théel, 1886)

See: Mortensen, 1927: 382–383, figs 226, 227; Heding, 1942: 9–10, fig. 9.

SAMPLE. ES 105(1). [1600 m]

DISTRIBUTION. Cosmopolitan, 694–5108 m. The deepest record from the South Atlantic referred to as *M. lactea* var. *spinosa* by Heding, 1940 should probably be more appropriately assigned to *M. candelabra* Hérouard, 1923. The deepest record would then become 4400 m in the North Atlantic (Sibuet, 1977). However, *M. lactea* is more abundant at shallower depths, usually at about 1500 m in the NE. Atlantic (Hérouard, 1923).

Pseudostichopus villosus Théel, 1886

See: Théel, 1886*a*: 170–171; Heding, 1940: 353–360.

SAMPLES. ES 6(1), AT 121(1). [2910 m]

DISTRIBUTION. Cosmopolitan; generally between 2515 and 7000 m, but also taken off Guadeloupe at 896 m (Deichmann, 1930). The wide bathymetric range may reflect the taxonomic difficulties evident in this genus.

REMARKS. Although Heding (1940) revised the genus *Pseudostichopus* placing *P. villosus* in the genus *Molpadiodemas* and the family Gephyrothuriidae, several authors have continued to record *villosus* under the generic name *Pseudostichopus* in the family Synallactidae (Madsen, 1953; Hansen, 1956, 1975; Lemche *et al.*, 1976; Sibuet, 1977). In view of the doubts concerning Heding's classification we have continued to record *villosus* in *Pseudostichopus*.

There are two specimens in our samples. The one from AT 121 is 160 mm long and 80 mm wide at the widest point of an almost oval shape. The skin is thick, up to 4 mm, and white in colour although the holothurian is grey in general appearance owing to a layer of foreign particles, predominantly planktonic foraminifera, which cover the epidermis. Other fauna include benthic foraminifera, hydroids and what appear to be fungal hyphae. Much of the body is covered by a mucous layer which has to be scraped off to reveal the body surface. The tube-feet are numerous and are distributed all over the body. They are generally brown in colour and are about 1 mm long in their retracted state. No deposits were found apart from small irregular rods in the tentacles. The calcareous ring is well developed and made of 10 equal-sized, broad but rather short pieces.

The second specimen from ES 6 is exceedingly small, only 6 mm long, and is tentatively referred to this species. It has a posterior vertical furrow in which the anus is placed and is covered dorsally and laterally in numerous tube-feet. However the tube-feet are scarce on the ventral surface particularly in the middle part of the body. It has 17 tentacles which have small irregular rods but is otherwise devoid of skin deposits.

Comparison of the large individual with specimens of *P. atlanticus* R. Perrier, 1902 from the Porcupine Seabight confirms Deichmann's (1930, p. 88) proposal that Hérouard's (1923) record of *P. villosus* should be referred to *P. atlanticus.*

Deep-sea photographs of *P. villosus* can be found in Lemche *et al.* (1976, pls 21d, 22a).

Large populations of bacteria have been found in the gut of *P. villosus* (Bianchi, Scoditti & Bensoussan, 1979). This holothurian is also able to select for less dense particles when feeding and assimilates about 20% of the organic matter ingested (Sibuet *et al.,* 1982).

Family **STICHOPODIDAE**

Stichopus tremulus (Gunnerus, 1767)

See: Mortensen, 1927: 389–390, fig. 228: 1, fig. 231.

SAMPLES. ES 113(1), AT 133(20), AT 194(6), GT 7(3). [168–689 m]

DISTRIBUTION. North-east Atlantic, Norway to the Canaries; generally 240–1918 m but may rise to as shallow as 20 m off Scandinavian coasts.

REMARKS. The ecology of *S. tremulus* is fairly well known owing to its occurrence at shallow depths (for a review see Jespersen & Lützen, 1971). *S. tremulus* is liable to infection by several parasites including the bizarre gastropod *Enteroxenos* (see Lützen, 1979) which is also found in deep water specimens (D.S.M.B., unpublished data).

S. tremulus is a selective deposit feeder showing a preference for the faecal pellets of other animals and sediment aggregates with a higher organic content than the surface sediment (Hauksson, 1979).

Order **ELASIPODA**
Family **DEIMATIDAE**

Oneirophanta mutabilis mutabilis Théel, 1879

See: Hansen, 1975: 24–32, text-figs 2–5, 94: 2, 96, pl. 8, figs 1–2, pl. 11, fig. 2, pl. 13, fig. 3.

SAMPLES. ES 28(3), AT 119(1), AT 121(15), ES 129(3), AT 130(1), ES 136(1), ES 137(1), ES 164(1), SWT 15(5). [2900–4810 m]

DISTRIBUTION. Cosmopolitan; the bathymetric range generally lies between 3200 and 6000 m. Specimens have been taken as shallow as 1804 m in the mid-North Atlantic (Hérouard, 1923) and 500 m off the Andaman Islands, Indian Ocean (reported in Deichmann, 1930), although it should be noted that in the latter case the bottom is particularly steep in this area. The new records extend the range at which *O. mutabilis mutabilis* is abundant up to 2900 m.

REMARKS. This holothurian is associated with a variety of animals including parasitic gastropods (Bouchet & Lützen, 1980), cyclopoid copepods (Humes, 1974), and parasitic amphipods that have been found within the intestine (D.S.M.B., unpublished data).

REPRODUCTION. The sexes are separate, the eggs of females reaching 950 μm diameter (Hansen, 1975; Tyler *et al.,* in press) although most are <400 μm. Specimens of *O. mutabilis affinis* Ludwig, 1894 collected by the *Galathea* in the Pacific off Central America were found to show intra-ovarian brood protection. This has not been found in females collected from the NE. Atlantic (D.S.M.B. and P.A.T. pers. obs.).

It is of interest that females appear to undergo oogenesis by a pattern typical of holothurians, but there is little evidence of spermatogenesis in males. We have found no ripe males and only very occasionally do we find males in the earliest stages of spermatogenesis. A similar feature is seen in the related species *Deima validum* (Tyler *et al.,* in press).

Family **LAETMOGONIDAE**

Laetmogone violacea Théel, 1879

See: Hansen, 1975: 58–61, text-figs 21–22, pl. 8, fig. 8, pl. 11, figs 9–10.

Samples: SBC 64(1), ES 99(1), AT 162(4), ES 178(19), SWT 12(2), GT 11(2), GT 17(16). [992–1400 (3000) m]

Distribution. Almost a cosmopolitan distribution but not recorded from the W. Atlantic or E. Pacific; 225–1804 m. Hansen (1975) considered that the distribution may be dependent on the dispersal of larvae by deep-sea currents.

The present records fall within the expected bathymetric range, except for SWT12 taken at the base of the extremely steep continental slope to the west of the Porcupine Bank. The two specimens were in good condition and not the result of contamination from a previous haul. They may represent an extension in the bathymetric range of *L. violacea*, or result from some downslope process off the Porcupine Bank.

Remarks. Many specimens bore the marks of the commensal polychaete *Eunoë laetmogonensis* on their ventral surface (Kirkegaard & Billett, 1980). *L. violacea* is bioluminescent, emitting light from the body wall and from the tips of the dorsal papillae (Herring, 1974).

Reproduction. Maximum egg size is up to 400 µm, suggestive of direct development, with no seasonal periodicity. For holothurians, this is considered an 'intermediate' egg size between the small eggs (<200 µm) of those with planktotrophic development, and the large eggs (>600 µm) of those with direct development. These eggs may give rise to an 'abbreviated' lecithotrophic larva the development of which, although not greatly prolonged, is sufficiently long to allow dispersal of larvae that need to feed away from the adult population (Tyler *et al.*, in press).

Benthogone rosea Koehler, 1896

See: Hansen, 1975: 48–49, fig. 15.

Samples. AT 157(19), AT 161(17). [1745–2055 m]

Distribution. Eastern Atlantic, SW. Pacific, W. Indian Ocean; 1103–2480 m.

Although the lower bathymetric limit was increased to 4100 m by Sibuet (1977) from material taken at BIOGAS st. 3, Bisol *et al.* (1984) state that *B. rosea* was taken only at BIOGAS st. 1 (1800–2200 m). The present records extend the geographic distribution in the NE. Atlantic and confirm that *B. rosea* is often common at about 2000 m.

Remarks. When captured *B. rosea* often eviscerates and releases copious amounts of slime. It bioluminesces weakly, generally on the dorsal surface (Herring, 1974). The organic composition of the body-wall is similar to that of shallow-water holothurians (Sibuet & Lawrence, 1981) and it is able to select detrital particles that are rich in bio-available compounds (Khripounoff & Sibuet, 1980). *B. rosea* appears to have a patchy distribution on the bottom (Sibuet, 1977).

Reproduction. Maximum egg size is 750 µm, suggestive of direct development and there is no evidence of reproductive seasonality (Tyler *et al.*, in press).

Family **PSYCHROPOTIDAE**

Psychropotes depressa (Théel, 1882)

See: Hansen, 1975: 106–111, figs 43–44, pl. 7, figs 1–3, pl. 12, fig. 8, pl. 14, figs 1–2.

Samples. ES 28(1), AT 121(3), ES 147(1), AT 181(1), ES 184(1), SWT 27(1). [2220–2965 m]

Distribution. Throughout North Atlantic, Gulf of Guinea, Japan, Gulf of Panama and off Chile; probably cosmopolitan ranging over deeper bathyal and upper abyssal zones; 957–4060 m.

Remarks. Pawson (1982) noted a patchy distribution for *P. depressa* in the Tongue of the Ocean, Bahama Islands.

Psychropotes longicauda Théel, 1882

See: Hansen, 1975: 115–126, figs 49–54, pl. 7, figs 4–6, pl. 12, fig. 7.

SAMPLES. AT 121(1), SWT 12(1), SWT 5(3). [2910–4810 m]

DISTRIBUTION. Cosmopolitan; 2210–5173 m.

REMARKS. This holothurian is often infected by the sporozoan parasite *Ixoreis psychropotae* (Massin, Jangoux & Sibuet, 1978). Its body-wall organic composition is similar to that of shallow water holothurians (Sibuet & Lawrence, 1981) and it is able to select particles of nutritional value (Khripounoff & Sibuet, 1980) including spores and pollen (Kozyar *et al.*, 1974). A pelagic specimen referred to a new nominal sp., *Nectothuria translucida* Belyaev & Vinogradov, 1969, was taken using a closing plankton net at 4940 to 5930 m in the Pacific Ocean (Belyaev & Vinogradov, 1969). This was subsequently shown to be a juvenile of *P. longicauda* by Hansen (1975).

Benthodytes lingua R. Perrier, 1896

See: Hansen, 1975: 80–82, fig. 29, pl. 9, figs 3–5, pl. 12, figs 2–3.

SAMPLES. ES 27(1), ES 28(2), AT 121(1). [*c*. 2900–2910 m]

DISTRIBUTION. North and South Atlantic; 860–3192 m.

REMARKS. The specimens are between 120 and 150 mm long and have a gelatinous skin with cross-shaped spicules. They are pale brown dorsally, faint purple laterally, and dark brown ventrally. This species can reach a length in excess of 300 mm and has been seen to have a patchy distribution on the bottom in the W. Atlantic (Pawson, 1982).

Family **ELPIDIIDAE**

Peniagone azorica von Marenzeller, 1893

See: Hansen, 1975: 138–142, fig. 63, pl. 10, figs 1–3.

SAMPLES. ES 2(109), ES 5(1), ES 6(43), ES 8(2), ES 10(1), ES 27(81), ES 28(38), ES 34(53), ES 52(5), ES 53(1), ES 54(14), ES 55(14), ES 56(8), ES 59(?juvenile 1), ES 110(5), ES 111(2), AT 114(2), ES 118(1), AT 119(16), ES 120(4), AT 121(76), ES 122(21), ES 129(1), AT 138(81), AT 139(64), ES 147(5), AT 154(121), ES 164(1), AT 167(11), ES 176(3), AT 219(1), SWT 11(166), SWT 13(2), SWT 16(191), SWT 27(648). [1991–3463 m]

DISTRIBUTION. *P. azorica* has a rather curious distribution. It is present in the NE. Atlantic between 1385 and 4020 m but has also been found in the Kermadec Trench between 2640 and 8210 m (Hansen, 1975). It has been photographed in other Pacific deep-sea trenches (Lemche *et al.*, 1976) and possibly within the Romanche Trench in the Atlantic (Heezen *et al.*, 1964). The present records confirm that this species is common between 2000 and 3000 m in the NE. Atlantic (Hérouard, 1923; Le Danois, 1948).

REMARKS. The specimen recorded at ES 5 (763 m) was undoubtedly a contaminant from a previous haul. The large differences in the number of specimens taken from hauls on or near 54°40′N, 12°16′W in the southern Rockall Trough may indicate a patchy distribution for this holothurian.

REPRODUCTION. Juveniles (<*c*. 30 mm body length) were relatively rare, the body length frequencies of all except one sample being unimodal, peaking between 42 and 53 mm. The ES 27 sample was bimodal with a peak of juvenile frequencies at *c*. 20 mm length as well as an adult peak at *c*. 47 mm. We interpret this size structure as suggesting infrequent, spasmodic recruitment to a slowly-growing adult population.

The sexes are separate. Maximum egg size observed is about 350 µm, a somewhat smaller egg size than most of the deep-sea holothurians studied to date (Tyler *et al.*, in press). These authors suggest possibly 'abbreviated' lecithotrophic development, as for *Laetmogone violacea*. Unspawned eggs appear to undergo phagocytic breakdown.

Peniagone diaphana (Théel, 1882)

See: Hansen, 1975: 153–155, fig. 71, pl. 10, figs 7–8.

SAMPLE. SWT 15(1). [4810 m]

DISTRIBUTION. Described originally from a single specimen taken in the Australian Bight by the *Challenger* Expedition (Théel, 1882), several more specimens were sampled later in the NE. Atlantic (Hérouard, 1899, 1902, 1923). More recently specimens have been observed from submersibles in the W. Atlantic (Pawson, 1976) and NE. Pacific (Barnes *et al.*, 1976). The wide separation of these records is probably due to the difficulties in sampling this benthopelagic holothurian (see below) which otherwise has a cosmopolitan distribution; 1900–5600 m.

REMARKS. Although Hérouard (1923) took some specimens of *P. diaphana* in pelagic nets it was not until dense populations were observed from a submersible (Barnes *et al.*, 1976) that its benthopelagic lifestyle was known. *P. diaphana*, which is capable of weak swimming movements, lives in the water column generally within 100 m of the sediment surface. Pelagic nets (RMT 1+8, Roe & Shale, 1979) towed between 5 and 100 m above the sediment surface at abyssal depths in the NE. Atlantic have taken some excellent specimens of *P. diaphana* (Billett *et al.*, in press). Barnes *et al.* (1976) noted that the distribution of *P. diaphana* could be patchy. Although only one specimen was taken in SWT 15, another trawl on the Porcupine Abyssal Plain at 4510 m took 339 specimens (Billett *et al.*, in press). *P. diaphana* was the most abundant holothurian taken below 4000 m in the Bay of Biscay during the BIOGAS cruises (Sibuet, 1977).

The feeding activities of this species were observed by Barnes *et al.* (1976). They concluded that *P. diaphana* survives on a low-energy budget, the sedimentary material in the gut containing very little organic matter.

REPRODUCTION. The sexes are separate. Maximum egg size is *c.* 350 μm, as in *P. azorica*, indicating that some form of 'abbreviated' early development may occur. Unspawned eggs appear to undergo phagocytic breakdown, again as with *P. azorica* (Tyler *et al.*, in press).

Kolga hyalina Danielssen & Koren, 1879

See: Hansen, 1975: 170–171, fig. 123; Billett & Hansen, 1982: 804–806, fig. 2.

SAMPLE. ES 172(15). [2910 m]

DISTRIBUTION. Arctic, North Atlantic, Antarctic, Pacific off Japan. Probably cosmopolitan, its patchy geographic distribution due, in part, to its unusual life-history (Billett & Hansen, 1982); 1510–4850 m.

REMARKS. Although fairly abundant in the one sample taken in the southern Rockall Trough in May 1980, *K. hyalina* was absent from all other samples at that station, including two taken in the same year. All the specimens were small and of a similar size (4–5 mm). Billett & Hansen (1982) found that *K. hyalina* exhibited characteristics typical of r-selected, or physically controlled, fauna (Sanders, 1979), which resulted in the periodic occurrence of a large number of juveniles in localised areas. Owing to predation the population may not persist for long. *K. hyalina* forms dense aggregations which may be caused by the patchy distribution of detrital material seen to collect on the sediment surface at certain times of the year (Billett *et al.*, 1983). *K. hyalina* is bioluminescent, emitting a bright blue light (Herring, 1974).

REPRODUCTION. *K. hyalina* reaches maturity at a very early age. The smallest specimens sampled (3 mm) have developing gonads (Billett & Hansen, 1982). The largest egg size is 180 μm indicating indirect development.

Order **APODIDA**

Family **SYNAPTIDAE**

Labidoplax southwardorum Gage, 1985

See: Gage, 1985: 255–261, figs 1, 3: A, D–F

SAMPLES. ES 20(1), ES 27(9), ES 28(1), SBC 48(1), ES 56(9), ES 57(3), SBC 58(2), ES 59(7), SBC 61(1), SBC

63(?2), SBC 67(1), ES 99(1), ES 105(2), ES 111(4), ES 118(2), ES 129(7, ?3), ES 135(1, ?1) ES 137(23), ES 140(?1), ES 143(4), ES 147(11), ES 152(2), ES 164(7), ES 169(8), ES 172(2), SBC 174(?1), ES 176(22), ES 180(9), ES 184(13), ES 190(3). [*c*. 1000–292 m]

DISTRIBUTION. This species is apparently widely distributed in the sediments of the Rockall Trough.

REMARKS. This is a small-sized species possessing eleven tentacles and body-wall deposits consisting of anchor-plates and anchors typical of the genus *Labidoplax*. However, the anchor plates are not only larger than those known from other species of this genus, which in any case is previously unknown in the deep sea, but also are unusual in being somewhat greater in length than the corresponding anchors, the size ranges being 129–207 and 110–188 µm, respectively. As preserved, they overlap making the skin stiff and inflexible; however, this must have resulted from contraction of the body, otherwise it would not be possible for these deposits to function normally (see Mortensen, 1927). In number of tentacles and absence of accessory deposits, *L. southwardorum* resembles the coastal *Labidoplax buski* (McIntosh, 1866). The latter is known from the coast of Norway to the Mediterrranean, and off the Carolinas in the western Atlantic, to 550 m depth. However, although its anchors are similar in size, the anchor plates are distinctly smaller.

None of the specimens was complete, most consisting only of the oral ring, measuring 0·9–1·6 mm diameter. This probably resulted from autotomy on disturbing the animal rather than from the cutting edge of epibenthic sledge, because intact animals were not recovered from the box-core samples.

The tentacles bear two pairs of lateral digits that, although contracted in the present specimens are probably extended in life serving to gather material from the sediment surface. The gut in the few body fragments usually appeared distended with contained sediment.

Labidoplax similimedia Gage, 1984

See: Gage, 1985: 255–261, figs 2, 3, B–D.

SAMPLES. ES 34(1), ES 147(1), ES 169(2), ES 172(1), ES 176(1), ES 190(2), ES 200(1), ES 204(2). [2220–2925 m]

DISTRIBUTION. Hebridean slope, central and southern areas of the Rockall Trough.

REMARKS. This small-sized species occurred in samples together with *Labidoplax southwardorum. L. similimedia* is distinguishable by both the considerably smaller size of the anchor-plates and anchors in the body wall, and the presence of rod deposits with branched ends within the tentacles. These latter deposits appear similar to those of *Labidoplax media* Östergren, 1905 (see also Gotto & Gotto, 1972). *L. media* is a coastal species known only from scattered records off Norway, the British Isles and the Mediterranean down to 95 m depth. However, the present species possesses only 11 tentacles rather than the 12 of *L. media.* All specimens were incomplete, consisting either of the anterior end of the body with the oral ring, 0·8–1·4 mm in diameter, or a body fragment.

As with *L. southwardorum,* this may be the result of autotomy when disturbing the animal, while the crowding of the deposits in the body wall again suggests this is an artefact reflecting contraction of the body-wall musculature.

Protankyra brychia (Verrill, 1885)

See: Madsen, 1953: 151–173, fig. 1.

SAMPLES. ES 32(1), ES 56(1), ES 152(1), ES 164(1), ES 169(1), ES 172(2), ES 180(1), ES 185(2), SBC 188(1), ES 207(2). [2871–2925 m]

DISTRIBUTION. Probably throughout the deep Atlantic between 47°N to 16°S, where it has been recorded as either *brychia* or *abyssicola* Théel, 1886*a,* the two names being synonymised by Deichmann (1940); 1688–4990 m. Although Clark (1920) indicates that *P. pacifica* (Ludwig, 1894), obtained by the *Albatross* from off Panama, is conspecific with *P. abyssicola,* Deichmann (1940) and Madsen (1953) consider *pacifica* should be maintained as a distinct species.

Only two specimens were intact, one measuring 32 mm and the other 38 mm long. Another was in two halves, together measuring 26 mm. The remainder were incomplete, lacking either the anterior or posterior end. Most were strongly contracted but otherwise in good condition. Hence, the body lengths measured probably do not reflect their size in life. Colour ranged from a yellow-orange, particularly evident in the tentacles, to a greyish-white colour. The body wall was wrinkled, probably as a result of contraction of the powerful radial and longitudinal musculature.

REMARKS. Examination of the skin of several small specimens in the present collection revealed the presence of not only the anchors and plates typical of this species, though slightly smaller than usual, but also curved rods and auricularia-like wheels. The curved rods were of widely varying shape, sometimes toothed along their length and always more or less branched at the ends. They were scattered in the body wall, and particularly abundant in the tentacles. The presence of wheels is surprising in postlarval stages, although such deposits have long been known to occur in synaptid auricularia larvae (Semon, 1888; Chun, 1896). They measured 84–99 µm in diameter with 12–18 spokes radiating from a wide hub measuring 32–40% of wheel diameter and possessing a conical protruberance in the centre. Around the rim were *c.* 100 minute inwardly pointing teeth. Both in the latter respect, and in their size and other characteristics, these wheels appear closely similar to those described by Pawson (1971) in the giant pelagic larva, 'Auricularia nudibranchiata' from deep water off New Zealand.

On the smallest specimen examined, 4·5 mm long, but lacking the posterior end, the plate apertures were always untoothed but otherwise resembled the developing plates, also untoothed, on larger specimens. The size and degree of development of the anchors and plates seemed to be related to body size, those of the largest specimens examined (37 mm long, but severely contracted) up to 500 µm and 460 µm in length, respectively. On the smallest specimen examined (measuring 4·5 mm) anchors measured up to 376 µm and plates up to 285 µm, while on specimens of intermediate size anchors and plates ranged between these two sets of values. In addition, in the tentacles and body wall of the largest specimen the curved rods were reduced to single unbranched rods or smooth oval particles. A similar relationship between body size of the anchors and anchor-plates was noted in the affiliated species *Rynkatorpa hickmani* described by Rowe & Pawson (1967). In view of this evidently body-size-related variability in the deposits, a revision of *Protankyra* and related taxa is necessary together with checking of other described species from the deep sea. Moreover, the presence of closely similar wheels on the very large larva 'Auricularia nudibranchiata', specimens of which have been obtained up to 15 mm long (Ohshima, 1911) and for which the adult is unknown, suggests a possible link with the genus *Protankyra.*

REPRODUCTION. The long, slightly branched gonads of the largest specimen, length 37 mm, from ES 185 and that from ES 32, length 26 mm, were removed and each found to contain a number of large, roughly globular, vitellogenic oocytes. Measurements of these gave a unimodal distribution of size frequencies peaking at about 100 µm diameter. The largest oocytes found were ovoid or sausage-shaped and measured up to around 200 µm in length.

Family **MYRIOTROCHIDAE**

Myriotrochus bathybius H. L. Clark, 1920

See: H. L. Clark, 1920: 126–127, pl. 4, fig. 3; Gage & Billett, in press.

SAMPLES. ES 6(1), ES 27(1), ES 56(3), SBC 68(1), ES 118(1), ES 129(2), ES 137(1), ES 147(3), ES 152(1), ES 164(2), ES 169(2), ES 172(2), ES 180(2), ES 184(1), SBC 188(1), ES 190(2), ES 204(1), ES 207(3). [*c.* 1800–2925 m]

DISTRIBUTION. The only published records are from the type locality in the eastern equatorial Pacific, 3666 m, and NE. Pacific off Oregon although *M. bathybius* was also taken by the

Galathea in the Indian and South Atlantic Oceans (Dr Bent Hansen, Copenhagen, personal communication) and by the *Discovery* at 3680–4104 m depth in the Porcupine Seabight. An unidentified *Myriotrochus* sp. recorded by Cherbonnier (1969) from 485 m off NW. Spain is likely to be a related species (see Gage & Billett, in press).

REMARKS. Gage & Billett (in press) record this species for the first time in the North Atlantic, occurring both in unpublished *Discovery* trawlings from the Porcupine Seabight at 3680–4104 m depth, 6 specimens, and in the present samples from Rockall. The fairly wide range in variation seen in measurements made on the wheels of the present Rockall specimens was found by Gage & Billett to encompass both that of the two specimens described by Clark (1920) and the *Discovery* specimens from the Porcupine Seabight.

A 2·9 mm long specimen of a probably parasitic species of the gastropod family Eulimidae was found lying within the gullet of one large *M. bathybius* from Rockall.

REPRODUCTION. Maximum size of oocytes in the paired, branched female gonads was 160 μm (Gage & Billett, in press). On the tentacles and oral disc of three of the Rockall specimens and one of the two *Discovery* specimens from the Porcupine Seabight were found numerous, small, four- or five-tentacled forms with an attaching disc. They were all approximately the same size and it is possible that these are brooded larvae at the Pentactula stage.

Myriotrochus giganteus H. L. Clark, 1920

See: Clark, 1920: 127–128, pl. 4, fig. 4; Belyaev & Mironov, 1981: 179–170, fig. 4, tables 4, 5 (as *M. macquoriensis* [sic]).

SAMPLES. ES 137(1), ES 164(2), ES 207(1). [2898–2925 m]

DISTRIBUTION. The only published records are from the type locality in the eastern equatorial Pacific, 3666 m and from the NE. Pacific off Oregon, 3300–3800 m. However, Gage & Billett (in press) synonymise *Myriotrochus* sp. ex gr. *macquoriensis-giganteus* Belyaev & Mironov, 1982 from the eastern equatorial Pacific at 3370–3400 m, with *M. giganteus*. It seems probable that *M. giganteus* has a cosmopolitan distribution at abyssal depths in the world ocean.

REMARKS. The only complete specimen was that obtained from ES 207. It measured 27·5 mm in length with a slightly inflated anterior section of the body. The calcareous ring measured 3 mm in diameter, while that of the other, incomplete, specimens ranged from 2·8 to 4 mm. A detailed description of the present specimens, including details of the body wall deposits and the morphology of the plates of the calcareous ring, is given by Gage & Billett (in press), who also discuss and justify the synonymy with the nominal species described by Belyaev & Mironov 1982).

REPRODUCTION. A pair of female, tubular-shaped gonads was found in the specimen from ES 207. The few, irregular-shaped vitellogenic eggs that could be seen inside, maximum diameter 211 × 169 μm, suggests that some form of indirect early development occurs.

Myriotrochus sp.

See: Gage & Billett (in press).

SAMPLES. ES 34(1), ES 197(1), ES 200(2), AT 221(9), [1605–2515 m]

DISTRIBUTION. This species was not found in the many hauls from depths greater than 2515 m in the Rockall Trough.

REMARKS. None of the specimens obtained were complete; although in one only the tip of the posterior end appeared to be missing. The body length of this specimen was 18·7 mm with a maximum width of 3·4 mm just behind the oral ring. The anterior third of the body was rough-surfaced with numerous irregular short processes whilst the posterior part was smooth. The body lacked pigmentation, and possessed 12 tentacles, now retracted, each possessing two pairs of short rounded lobes. The wheels were of typical myriotrochid form; details of various wheel measurements are given in Gage & Billett (in press) together with a description of the morphology of the plates of the calcareous ring.

Prototrochus zenkevitchi (Belyaev, 1970) subsp.

See: Gage & Billett (in press).

SAMPLES. ES 6(2), ES 10(1), ES 15(2), ES 20(11), ES 34(?1, 3), ES 57(1), SBC 64(2), SBC 67(1), ES 105(2), ES 129(4), ES 135(1), ES 137(1), ES 147(1), SBC 155(7), ES 169(1), ES 172(3), ES 176(12), ES 190(1), ES 197(30), ES 200(8), ES 207(2). [*c*. 1000–2921 m]

DISTRIBUTION. Widely distributed in the Rockall Trough, and with a wide bathymetric range in soft mud and ooze.

REMARKS. This small species is evidently fragile as most specimens consist of the anterior end only. From the body length of the few intact specimens, Gage & Billett (in press) estimate the likely maximum size as *c*. 10 mm. The average inferred length was a little less than 5 mm. In the body wall there are numerous wheel-like deposits typical in form to those of the Myriotrochidae. However, there are 10 tentacles, rather than 12 as defined for the genus *Myriotrochus* by Belyaev & Mironov (1982), so the taxon must be placed in the recently established genus *Prototrochus* Belyaev & Mironov, 1982 along with other previously described species with 10 tentacles. Gage & Billett show the present material to have close affinity to *P. zenkevitchi* Belyaev, 1970, described from material trawled from various trenches in the NW. Pacific. A degree of variation was evident between samples from different trenches in terms of measurements of the typical myriotrochid wheels present, while a separate subspecies was erected for one population in which wheels were very few or absent. Later a further subspecies, *M. zenkevitchi atlanticus* Belyaev & Mironov, 1977 was described from the Romanche Trench off Senegal. The generally small body size of the present material might be interpreted as reflecting numerical dominance by juveniles in the population. However, no size-related correlations in wheel parameters were apparent from extensive measurements, and Gage & Billett therefore concluded that the differences evident in wheel parameters, compared to those for the previously described subspecies of *Prototrochus zenkevitchi,* justifies taxonomic distinction of the Rockall material.

In view of the sediment-filled gut that distended the body of complete specimens, it seems that this small species probably feeds on the bottom deposit.

Myriotrochidae gen. et sp.

See: Gage & Billett (in press).

SAMPLES. ES 56(1), ES 57(1), ES 105(2), ES 135(2), ES 143(1), ES 152(1), ES 169(1), ES 172(1), ES 180(1), ES 197(1), ES 204(1), ES 207(1). [1690–2921 m]

DISTRIBUTION. Probably with a distribution in Rockall similar to that of *Prototrochus zenkevitchi.*

REMARKS. All but one of the specimens are minute, varying in length from 1·3 to 2·3 mm in length. The body wall is densely covered with curved, pointed rods in addition to some scattered, small wheels (35–60 µm diameter) of the typical myriotrochid design. There are 10 tentacles, each with two, possibly more, pairs of lobes and with curved rods at their base. The short, spiny body has a pointed posterior end reminiscent of aplacophoran molluscs, and Gage & Billett (in press) speculate that these holothurians have a similar mode of life in the superficial layer of the sediment.

Prototrochus sp. aff. *P. minutus (*Östergren, 1905)

See: Gage & Billett (in press).

SAMPLE. SBC 155(1). [1330 m]

DISTRIBUTION. Known only from the N. Bay of Biscay.

REMARKS. This specimen, 2·4 mm long, was collected from the Whittard Canyon, northern Bay of Biscay. It resembles the previous specimens in having 10 tentacles of the same form, and has similar wheel deposits in the body wall. However, although rod-shaped deposits are found around the base of the tentacles, they are absent from the body wall. The specimen shows affinity to *Prototrochus minutus* (Östergren, 1905), a species known only from the Sea of Japan

(Östergren, 1905; Belyaev & Mironov, 1982), which has similar wheel and rod-shaped deposits, the latter only around the bases of the tentacles. The specimens also shows similarities to the Rockall individuals of *Prototrochus zenkevitchi*, particularly with reference to the structure of the wheels, but differs and in the occurrence of rods at the tentacle base at this size (1–3 mm). Both have a similar bathymetric and geographic distribution in this area.

Order **MOLPADIIDA**

Family **MOLPADIIDAE**

Cherbonniera utriculus Sibuet, 1974

See: Sibuet, 1974: 1443–1445, pl. 1.

SAMPLES. ES 2(107), ES 6(1550), ES 8(85), ES 10(4), ES 27(130), ES 28(3), ES 34(1), ES 55(194), ES 56(119), ES 57(17), SBC 58(1), ES 59(49), ES 111(65), ES 118(34), AT 119(33), ES 129(91), ES 135(49), ES 137(156), ES 140(114), ES 143(19), ES 147(122), SBC 150(1), ES 164(180), ES 169(87), ES 172(114), ES 180(275), ES 185(23), SBC 188(1), ES 190(7), ES 204(78), SBC 205(juvenile 1), ES 207(2). [2515–2925 m]

DISTRIBUTION. Previously known only from the Bay of Biscay; 2039–4251 m, on soft ooze.

REMARKS. The evident abundance of this species in the fine-meshed trawl hauls from depths greater than *c.* 2500 m indicates *Cherbonniera utriculus* may be found to be a common constituent of the deep-sea fauna in the NE. Atlantic. Because of its small size, it has probably either been overlooked or lost through the coarse meshes of the trawls used in previous deep-sea investigations. The sediment-filled gut suggests a deposit-feeding mode of life. The present records indicate that *C. utriculus* may have a patchy distribution.

REPRODUCTION. Our observations suggest the sexes to be separate, the gonads of females being short-branched tubules that are packed with eggs, measuring up to 200 µm in diameter (Tyler *et al.*, in press).

Molpadia blakei (Théel, 1886)

See: Heding, 1935: 72–76, pl. 4, figs 13, 14, pl. 5, figs 20, 21 (as *Paratrochostoma spiniferum*); Deichmann, 1940: 224–225, pl. 38, figs 6–8.

SAMPLES. ES 143(1), AT 144(1), SBC 150(?[juvenile] 1), AT 153(1), AT 167(1), AT 171(1), AT 175(1), ES 176(4), AT 177(2), AT 181(1), ES 184(1), ES 185(3), AT 191(3), AT 195(3), AT 198(1), AT 201(1), ES 202(1), ES 207(1), AT 219(4). [1991–2916 m]

DISTRIBUTION. North Atlantic, 1747–5270 m. *M. blakei* has been found to be particularly abundant in the Bay of Biscay at 3100 and 4100 m (Sibuet, 1977). Its apparent abundance at shallower depths in the Rockall Trough is probably due to sampling bias.

REMARKS. A thorough description of this species was given by Heding (1935) under the name *Paratrochostoma spiniferum*, who also noted its similarity to *Trochostoma blakei*. Deichmann (1940) during a revision of the Molpadiida synonymised the two names under the genus *Molpadia*.

Analysis of the gut content of this infaunal holothurian shows a close correlation to the surrounding sediment (Khripounoff and Sibuet, 1980).

Molpadia borealis Sars, 1858

See: Heding, 1935: 60–61, fig. 16, pl. 5, figs 6–7, pl. 8, fig. 3 (as *Trochostoma boreale*); 52–58, figs 13–14, pl. 4, figs 1–6, pl. 5, figs 1–5, pl. 8, fig. 1 (as *Trochostoma thomsonii*); Deichmann, 1936: 455–458, figs 4–6.

SAMPLE. AT 107A [*c.* 2000 m]

DISTRIBUTION. Arctic and the northernmost parts of the North Atlantic *c.* 225–1600 m. The present specimen represents the deepest and the most southerly record of *M. borealis*, which is usually distributed north of the Wyville-Thomson Ridge between 600 m and 1000 m where the water temperature is about 0·5°C. Its occurrence south of the Ridge but in deeper water supports Ludwig & Heding's (1935) proposal that the water temperature is important in limiting the distribution of this species.

REMARKS. The taxonomic characters of the Molpadiidae are so variable that it is not possible to describe satisfactorily a species without a full size distribution. The changes that occur with growth, even in the shape of spicules, have led in the past to the proliferation of many generic and specific names. The number of species was reduced to 10 within the single genus *Molpadia* by Deichmann (1940) for specimens taken in the Atlantic Ocean. Of the five nominal species originally described for the Arctic Ocean, Deichmann (1936) retained just two: *Molpadia borealis* (with synonyms *Ankyroderma jeffreysi* Danielssen & Koren, 1879, *Ankyroderma affine* Danielssen & Koren, 1872 and *Trochostoma thomsonii* Danielssen & Koren, 1878) and *Molpadia arctica* (Marenzeller, 1877).

The present specimen is in good condition and is 85 mm long, about half the size of a fully grown individual.

Discussion

In part 1 of the 'Echinoderms of the Rockall Trough' (Gage *et al.,* 1983) certain features of the bathymetric distribution of the sea lily, sea star, and brittle star species could be related to both the rather circumscribed area of the Rockall Trough and to its complex hydrography. The bathymetric range of adult specimens of many species was found to be narrower than the known worldwide bathymetric range. The geographic and bathymetric distributions of juveniles and post-larvae of some of the relatively abundant species were considerably greater than for the adult specimens. In addition, it was suggested that the higher species richness evident in the relatively small numbers of samples taken from the western side of the Rockall Trough, compared to the eastern side where sampling effort was heaviest, may be related to the conditions in this area which favour microphagous suspension feeders.

Some species of echinoids and holothurians show a similar restriction in their bathymetric distribution in the Rockall Trough in comparison to their known global bathymetric range, notably *Cidaris cidaris, Calveriosoma hystrix, Echinus alexandri, Spatangus raschi* and *Benthogone rosea.* In general the shallowest record of most species occurring in the Rockall Trough was considerably deeper than the shallowest depth those species are known to be able to attain. This may be the effect of temperature. Several species are known to occur at very shallow depths in the cold water at high latitudes, for example *Stichopus tremulus.* The progressive submergence of cold, deep ocean water towards low latitudes (Wüst, 1936) may lead to the progressive depression of the upper bathymetric limit of benthic animals. One species, *Molpadia borealis,* thought to be limited between 600 and 1000 m north of the Wyville Thomson Ridge by the 0·5° isotherm, was found at a much greater depth, i.e. in colder water, south of the ridge. Many species appear to have a lower bathymetric limit at about 2950 m, but this is merely due to the small area of the Rockall Trough deeper than 3000 m and to the lack of samples from this area.

The small number of records from the relatively few western stations compared to the numerous records emanating from the eastern side of the Rockall Trough would appear to reflect the greater sampling effort in the east. This is in contrast to the pattern found for the Asteroidea and Ophiuroidea, which included several suspension-feeding species. Echinoids are unknown as microphages, being either predators, or scavengers of material associated with the substratum, or deposit feeders like the majority of holothurians of which a few microphagous feeders are known. There were only two holothurian species from the present sampling that are probably suspension feeders: *Psolus pourtalesii* and *P. squamatus*; the latter occurred only on the Anton Dohrn Seamount at 713 m depth, whilst *P. pourtalesii* occurred only in a single haul from the Feni Ridge in 2190 m depth.

The other feature of the distribution of sea stars and brittle stars in Rockall that was noted by Gage *et al.* (1983), was of a broader postlarval/juvenile bathymetric range compared to that of adults. This was evident only amongst certain echinoids. These included the species of the genus *Echinus* and *Hemiaster expergitus.* Studies by Tyler & Gage (1984*a*) indicate that three *Echinus* species recorded from deep water in the Trough have both seasonal periodicity in breeding and probable planktotrophic development. Unfortunately, it has not proved possible to separate to species records of postlarvae belonging to *Echinus*. Therefore we cannot say for individual species whether settlement occurs over a greater area or wider range in depth than that of the breeding population. However, since the maximum depth (2910 m) for records of *Echinus* postlarvae well exceeded the bathymetric limits of the deepest living species (*E. affinis* and *E. alexandri*), a dispersion of larvae beyond the limits of the adult population seems likely for all three species.

The wide juvenile limits for the burrowing species *Hemiaster expergitus,* however, may be less significant. The discovery of a large specimen deeply burrowed in a box core indicates that surface skimming gear such as fine-meshed trawls and sled samplers will probably miss the more deeply burrowed adults whilst catching younger specimens that are able to burrow only superficially within the sediment.

Hansen (1975) suggests that the distributions of some bathyal and abyssal holothurian species are related to deep ocean currents. The egg size of most species is large, in some cases exceeding 1000 µm in diameter, reflecting their ability to subsist and develop independently of planktonic food for long periods and ensuring wide dispersal by currents. The noticeable poverty in holothurian records, particularly of elasipods on the western side of the Rockall Trough, may be related to the southwards-flowing current regime on the Feni Ridge, which is thought to mark the course of cold Norwegian Sea water overflowing into the North Atlantic via the Wyville Thomson Ridge (Jones *et al.,* 1970; Ellett & Roberts, 1973; Roberts, 1975). By contrast, in the east the bottom and slope water is more likely to have a southerly origin (Lonsdale & Hollister, 1979).

Summary

Eighteen species of sea urchin and thirty-three species of sea cucumber are identified from recent sampling conducted by the Scottish Marine Biological Association, chiefly from RRS *Challenger,* in the deep-sea areas lying to the west of the British Isles. The following species have not previously been recorded from the British seas (taken as including the northern Bay of Biscay area), although in some cases their presence there was predicted by Mortensen (1927).

Echinoidea
Holothurioidea
- *Aeropsis rostrata*
- *Psolus pourtalesii*
- *Abyssocucumis abyssorum*
- *Benthothuria funebris*
- *Labidoplax southwardorum*
- *Labidoplax similimedia*
- *Myriotrochus bathybius*
- *Myriotrochus giganteus*
- *Myriotrochus* sp.
- *Prototrochus zenkevitchi* subsp.
- *Prototrochus ?minutus*
- *Molpadia borealis*

	Upper limit	Lower limit
Echinoidea		
Hygrosoma petersii		2870–2965
Sperosoma grimaldii		2300–2910
Echinus affinis		2230–2450
Aeropsis rostrata	2550–1200[?1000]	
Echinosigra phiale		2377–2912
Holothurioidea		
Abyssocucumis abyssorum		4636–4810
Benthothuria funebris		2700–2996
Mesothuria cathedralis		2480–2540
Laetmogone violacea		1804–[3000]
Molpadia borealis		1600–2000

In this list the depths given are the minimum possible extensions of the previously known bathymetric limits. The figure in square brackets results from a record of specimens that may have been carried into deeper water by some down-slope process.

Postlarvae that could be identified only as belonging to the genus *Echinus* were collected from depths considerably in excess of the maximum depth recorded for the adults of the three species recorded from deep water. Although this is indicative of a wide bathymetric distribution of postlarvae, it remains unknown whether this applies to all three species found as breeding populations. Except for pourtalesiids, young stages of other echinoids, and of holothurian species recorded were but rarely, or never, found. It seems likely that this is related to both fecundity and mode of larval development. Whereas the *Echinus* species show the high fecundity associated with probable planktotrophy, the pourtalesiids displayed a lower fecundity and probable lecithotrophic mode of development. In the echinothuriids, and probably most of the holothurians, a lower fecundity is evident as a result of the often very large egg size. This may reflect an ability to subsist and develop independently of planktonic food for long periods, thus ensuring wide dispersal by currents.

In general terms, records of adults of the most abundant species are, like those of asteroids and ophiuroids, clustered well within the vertical range recorded over their, often circumoceanic, distribution.

Relationships needing further investigation

In the course of examination of the material we have found the following taxonomic relationships need further investigation as possible synonymies:

Benthothuria funebris R. Perrier, 1902 and
B. valdiviae Heding, 1940;
Paelopatides gigantea (Verrill, 1884) and
P. grisea R. Perrier, 1902.

Acknowledgements

We again express our gratitude to the officers and crews of RRS *Challenger* and RRS *Shackleton,* and to colleagues too numerous to name individually who participated in cruises and without whose cooperation and many kindnesses this work would not have been possible. We are very grateful to Miss B. Rae of Dervaig, Isle of Mull, for her help in sorting sled and box-core samples, Mrs Margaret Pearson of SMBA for her valuable assistance in the earlier stages of preparation of the present account, Mr G. L. J. Paterson of BM(NH) for undertaking many of the earlier holothurian identifications, and Miss Ailsa Clark of BM(NH) for her encouragement, provision of facilities and critical reading of the manuscript. The Scottish Marine Biological Association is grant-aided by the Natural Environment Research Council who have been generous in allocating to the SMBA cruise time on which the present records were made.

M.J. gratefully acknowledges support from the Wellcome-Carlsberg Foundation (Grant No. 33/82) during study leave at the British Museum (Natural History) in 1983 that was kindly arranged by Miss Ailsa Clark. P.A.T. gratefully acknowledges support from NERC research grant GR 35131 and DoE Commission PECD7/9/037.

References

Agassiz, A. 1880. Preliminary report of the Echini of the exploring expedition of H.M.S. *Challenger. Proc. Amer. Acad. Arts Sci.* **14:** 190–212.

—— 1881. Report on the Echinoidea dredged by H.M.S. *Challenger* during the years 1873–1876. *Rep. scient. Results Voy. Challenger* (Zool.) **3:** 1–321.

— 1883. Report on the results of dredging by the U.S. Coast Survey Steamer 'Blake', No. 24, Part 1, Report on the Echini. *Mem. Mus. comp. Zool. Harv.* **10**(1): 1–99.

Barnes, A. T., Quetin, L. B., Childress, J. J. & Pawson, D. I. 1976. Deep-sea macroplanktonic sea cucumbers: suspended sediment feeders captured from deep submergence vehicle. *Science* **194:** 1083–1085.

Belyaev, G. M. & Mironov. A. N. 1982. The holothurians of the family Myriotrochidae (Apoda): composition, distribution, and origin. [In Russian]. *Trudy Inst. Okeanol.* **117:** 81–120.

—— **& Vinogradov, M. E.** 1969. A new pelagic holothurian (Elasipoda, Psychropotidae) from the abyssal of the Kurile-Kamchatka Trench. [In Russian]. *Zool. Zh.* **48:** 709–716.

Bianchi, A. J.-M., Scoditti, P. M. & Bensoussan, M. G. 1979. Distribution des populations bactériennes hétérotrophes dans les sédiments et les tractus digestifs d'animaux benthiques recueillis dans la faille Vema et les plaines abyssales du Demerara et de Gambie. *Vie Mar.* **1:** 7–12 (Foundation Océanographique Riccard, Marseille).

Billett, D. S. M. & Hansen, B. 1982. Abyssal aggregations of *Kolga hyalina* Danielssen and Koren (Echinodermata: Holothurioidea) in the northeast Atlantic Ocean: a preliminary report. *Deep-Sea Res.* **29**(7A): 799–818.

——, **Lampitt, R. S., Rice, A. L. & Mantoura, R. F. C.** 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature, Lond.* **302:** 520–522.

——, **Hansen, B. & Huggett, Q. J.** (in press). Pelagic Holothurioidea (Echinodermata) of the northeast Atlantic. *In:* Keegan, B. F. & O'Connor, B. [Eds] Proc. int. Conf. Echinoderms, Galway, 1984. Balkena, Rotterdam.

Bisol, P. M., Costa, R. & Sibuet, M. 1984. Ecological and genetical survey on two deep-sea holothurians: *Benthogone rosea* and *Benthodytes typica. Mar. Ecol. Prog. Ser.* **15:** 275–281.

Bouchet, P. & Lützen, J. 1980. Deux gastéropodes parasites d'une Holothurie Élasipode. *Bull. Mus. natn. Hist. nat. Paris* (4) **2:** 59–75.

Cherbonnier, G. 1941. Étude anatomique et biogéographique sur deux *Cucumaria* abyssaux: *C. abyssorum* Théel et *C. albatrossi* n.sp. *Bull. Mus. natn. Hist. nat. Paris* (2) **13:** 93–103.

—— 1969. Echinodermes récoltés par la *Thalassa* au large des côtes ouest de Bretagne et du Golfe de Gascogne (3–12 Aout 1967). *Bull. Mus. natn. Hist. nat. Paris* (2) **41**(1): 343–361.

Chesher, R. H. 1963. The morphology and function of the frontal ambulacrum of *Moira atropos* (Echinoidea: Spatangoida). *Bull. var. Sci. Gulf Caribb.* **13:** 549–573.

Chun, C. 1896. Atlantis, Biologische Studien über pelagische Organismen *Auricularia nudibranchiata. Bibltha zool. II* **19:** 55–75.

Clark, H. L. 1907. The apodous holothurians. *Smithson. Contr. Knowl.* **35** No. 1723, 231 pp.

—— 1914. Hawaiian and other Pacific Echini. The Spatangina. *Mem. Mus. comp. Zool. Harv.* **46:** 81–283.

—— 1920. Tropical Pacific Holothurioidea. *Mem. Mus. comp. Zool. Harv.* **39:** 115–154.

—— 1941. Report on the scientific results of the Atlantis Expeditions to the West Indies, under the joint supervision of the University of Havana and Harvard University. *Mem. Soc. Cubana Hist. Nat. 'Felipe Poey'* **15:** 1–154.

David, B. 1983. Isolément géographique de populations benthiques abyssales: les *Pourtalesia jeffreysi* (Echinoidea, Holasteroida) en Mer de Norvège. *Oceanologica Acta* **6:** 13–20.

—— (in press). A dynamic view of the growth of an abyssal sea urchin: changes in the plate array of *Pourtalesia miranda. In:* Keegan, B. F. & O'Connor, B. [Eds] *Proc. int. Conf. Echinoderms, Galway, 1984.* Balkema, Rotterdam.

Deichmann, E. 1930. The holothurians of the western part of the Atlantic Ocean. *Bull. Mus. comp. Zool. Harv.* **71**(3): 43–226.

—— 1936. The Arctic species of *Molpadia* (Holothuroidea) and some remarks on Heding's attempt to subdivide the genus. *Ann. Mag. nat. Hist.* **10**(17): 452–464.

—— 1940. Report on the holothurians, collected by the Harvard–Havana Expeditions 1938 and 1939, with a revision of the Molpadonia of the Atlantic Ocean. *Mem. Soc. Cubana Hist. Nat.* **14:** 183–240.

De Ridder, C. & Lawrence, J. M. 1982. Food and feeding mechanisms: Echinoidea. pp. 57–115 *In:* Jangoux, M. & Lawrence, J. M. [Eds] *Echinoderm Nutrition.* Balkama, Rotterdam.

Ebert, T. A. 1983. Recruitment in Echinoderms. pp. 169–203. *In:* Jangoux M. & Lawrence, J. M. [Eds] *Echinoderm Studies* Vol. 1. Balkema, Rotterdam.

Ekman, S. 1925. Holothurien. *Further zool. Results Swed. Antarct. Exped. 1901–3* **1**(6): 1–194.

—— 1927. Holothurien der deutschen Südpolar-Expedition, 1901–1903 aus der Ostantarktis und von den Kerguelen. *Dt. Südpol.-Exped.* **19**(Zool. 11): 359–419.

Einarsson, H. 1948. Echinoderma. *Zool. Iceland* **4**(70): 1–67.

Ellett, D. J. & Roberts, D. G. 1973. The overflow of Norwegian deep sea water across the Wyville Thomson Ridge. *Deep-Sea Res.* **20:** 819–835.

Fankboner, P. V. 1978. Suspension-feeding mechanisms of the armoured sea cucumber *Psolus chitinoides.* Clark. *J. exp. mar. Biol. Ecol.* **31:** 11–25.

Farran, G. P. 1913. The deep-water Asteroidea, Ophiuroidea and Echinoidea of the west coast of Ireland. *Scient. Invest. Fish Brch Ire.* **1912**(6): 1–66.

Gage, J. D. 1984. On the status of the deep-sea echinoids, *Echinosigra phiale* and *E. paradoxa*. *J. mar. biol. Ass. U.K.* **64:** 157–170.

—— 1985. New Synaptidae (Holothuroidea: Apoda) from the Rockall Trough. *J. mar. biol. Ass. U.K.* **65:** 225–261.

—— **& Billett, D. S. M.** (in press) The family Myriotrochidae Théel (Echinodermata: Holothurioidea) in the deep northeast Atlantic Ocean. *Zool. J. Linn. Soc.*

——, **Pearson, M., Clark, A. M., Paterson, G. L. J. & Tyler, P. A.** 1983. Echinoderms of the Rockall Trough and adjacent areas. 1. Crinoidea, Asteroidea and Ophiuroidea. *Bull. Br. Mus. nat. Hist.* (Zool.) **45**(5): 263–308.

Gotto, D. M. & Gotto, R. V. 1972. *Labidoplax media* Oestergren: a sea cucumber new to British and Irish waters, with observational notes. *Irish Nat.* **17:** 250–252.

Grassle, J. F., Sanders, H. L. Hessler, R. R., Rowe, G. T. & McLellan, T. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. *Deep-Sea Res.* **22:** 457–481.

Grieg, J. A. 1921 (& 1932). Echinodermata. *Rep. scient. Results Michael Sars N. Atlantic deep Sea Exped.* 3(2): 1–47.

Haedrich, R. L., Rowe, G. T. & Polloni, P. T. 1980. The megabenthic fauna in the deep sea south of New England, U.S.A. *Mar. Biol.* **57:** 165–179.

Hagstrom, B. E. & Lönning, S. 1961*a*. Studies of the species specificity of echinoderms. *Sarsia* **4:** 5–19.

—— **&** —— 1961*b*. Morphological and experimental studies on the genus *Echinus*. *Sarsia* **4:** 21–31.

Hansen, B. 1956. Holothurioidea from depths exceeding 6000 metres. *Galathea Rep.* **2:** 33–54.

—— 1975. Systematics and biology of the deep-sea holothurians. Part 1. Elasipoda. *Galathea Rep.* **13:** 1–262.

Harvey, R. & Gage, J. D. 1984. Observations on the reproduction and postlarval morphology of pourtalesiid sea urchins in the Rockall Trough area (NE Atlantic Ocean). *Mar. Biol.* **82:** 181–190.

Hauksson, E. 1979. Feeding biology of *Stichopus tremulus*, a deposit-feeding holothurian. *Sarsia* **64:** 155–160.

Heding, S. G. 1931. On the classification of the Molpadids (Preliminary notice). *Vidensk Meddr. dansk. naturh. Foren.* **92:** 275–284.

—— 1935. Holothurioidea. Part 1. Apoda, Molpadioidea, Gephyrothurioidea. *Dan. Ingolf-Exped.* **4**(9): 1–84.

—— 1940. Die Holothurien der deutschen Tiefsee-Expedition. II. Aspidochirote und Elasipode Formen. *Wiss. Ergebn. dt. Tiefsee-Exped. Valdivia* **24:** 317–375.

—— 1942. Holothurioidea. Part 2. Aspidochirota, Elasipoda, Dendrochirota. *Dan. Ingolf-Exped.* **4**(13): 1–39.

Heezen, B. C. & Hollister, C. D. 1971. *The face of the deep*. 659 pp. Oxford University Press, London.

——, **Bunce, E. T., Hersey, J. B. & Tharp, M.** 1964. Chain and Romanche fracture zones. *Deep-Sea Res.* **11:** 11–33.

Herring, P. J. 1974. New observations on the bioluminescence of echinoderms. *J. Zool. Lond.* **172:** 401–418.

Hérouard, E. 1899. Troisième note préliminaire sur les Holothuries provenant des dragages du yacht 'Princesse-Alice'. Revision de la sous-famille des Elpidiinae et description de nouvelles espèces. *Bull. Soc. zool. Fr.* **24:** 170–175.

—— 1902. Holothuries provenant des campagnes de la 'Princesse-Alice' (1892–1897). *Résult. Camp. scient. Prince Albert I* **21:** 1–61.

—— 1923. Holothuries provenant des campagnes des yachts *Princesse Alice* et *Hirondelle II* (1898–1915). *Résult. Camp. scient. Prince Albert I* **66:** 1–163.

Humes, A. G. 1974. New cyclopoid copepods associated with an abyssal holothurian in the eastern North Atlantic. *J. nat. Hist.* **8:** 101–117.

Imoaka, T. 1980. Observation on *Psolus squamatus* (Koren) from the Okhotsk Sea (Dendrochirota: Psolidae). *Publ. Seto mar. Biol. Lab.* **25:** 361–372.

Jensen, M. 1982. Morphology and classification of Euchinoidea Bronn, 1860—a cladistic analysis. *Vidensk. Meddr. dansk naturh. Foren.* **143:** 7–99.

Jespersen, Å. & Lützen, J. 1971. On the ecology of the aspidochirote sea cucumber *Stichopus tremulus* (Gunnerus). *Norw. J. Zool.* **19:** 117–132.

Jones, E. J. W., Ewing, M., Ewing, J. I. & Eittreim, S. 1970. Influences of Norwegian Sea overflow water on sedimentation in the northern North Atlantic and Labrador Sea. *J. Geophys Res.* **75:** 1655–1680.

Khripounoff, A. & Sibuet, M. 1980. La nutrition d'echinodermes abyssaux. 1. Alimentation des holothuries. *Mar. Biol.* **60:** 17–26.

Kirkegaard, J. B. & Billett, D. S. M. 1980. *Eunoë laetmogonensis*, a new species of polynoid worm, commensal with the bathyal holothurian *Laetmogone violacea*, in the North-East Atlantic. *Steenstrupia* **6:** 101–109.

Kozyar, L. A., Sokolava, M. N. & Zezina, O. N. 1974. Spores and pollen from higher plants in the nutrition of marine invertebrates. *Okeanologiya* **14:** 431–434.

Le Danois, E. 1948. *Les profondeurs de la mer*. 303 pp. Payot, Paris.

Lemche, H., Hansen, B., Madsen, F. J., Tendal, O. S. & Wolff, T. 1976. Hadal life as analysed from photographs. *Vidensk. Meddr. dansk naturh. Foren.* **139:** 263–336.

Lonsdale, P. & Hollister, C. D. 1979. A near bottom traverse of Rockall Trough: hydrographic and geologic inferences. *Oceanol. Acta* **2:** 91–105.

Ludwig, H. & Heding, S. G. 1935. Die Holothurien der deutschen Tiefsee-Expedition. I. Fusslose und Dendrochirote Formen. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **24:** 121–214.

Lützen, J. 1979. Studies on the life history of *Enteroxenos* Bonnevie, a gastropod endoparasitic in aspidochirote holothurians. *Ophelia* **18:** 1–51.

Madsen, F. J. 1953. Holothurioidea. *Rep. Swed. deep-Sea Exped.* **2** (Zool.) **12:** 149–173.

Marenzeller, E. von 1893. Contribution à l'étude des Holothuries de l'Atlantique Nord. *Résult. Camp. scient. Prince Albert I* **6:** 1–22.

Massin, C. 1982. Food and feeding mechanisms: Holothuroidea. pp. 43–55. *In:* Jangoux, M. & Lawrence, J. M. [Eds] *Echinoderm Nutrition*. Balkema, Rotterdam.

Massin, C., Jangoux, M. & Sibuet, M. 1978. Description d'*Ixoreis psychropotae* nov. gen. nov. sp. coccidie parasite du tube digestif de l'Holothurie abyssale *Psychropotes longicauda* Théel. *Protistologica* **14**(3): 253–259.

McCauley, J. E. & Carey, A. G. Jr. 1967. Echinoidea of Oregon. *J. Fish. Res. Bd Can.* **24:** 1385–1401.

Mironov, A. N. 1974*a*. New species of abyssal sea urchins of the genus *Echinosigra* (Echinoidea, Pourtalesiidae) [In Russian]. *Zool. Zh.* **53:** 1803–1806.

—— 1974*b*. Pourtalesiid sea urchins of the Antarctic and Subantarctic. (Echinoidea: Pourtalesiidae) [In Russian]. *Trudy Inst. Okeanol.* **98:** 240–252.

—— 1975. Mode of life of the pourtalesiid sea-urchins (Echinoidea: Pourtalesiidae) [In Russian]. *Trudy Inst. Okeanol.* **103:** 281–288.

—— 1978. The most deep-sea species of sea urchins (Echinoidea, Pourtalesiidae) [In Russian]. *Zool. Zh.* **57:** 721–726.

Mortensen, T. 1903. Echinoidea (Part I). *Dan. Ingolf-Exped.* **4**(1): 1–193.

—— 1907. Echinoidea (Part 2). *Dan. Ingolf-Exped.* **4**(2): 1–200.

—— 1909. Die Echinoiden der deutschen Sudpolar-Expedition 1901–1903. *Dt. Südpol.-Exped.* **11**(Zool. 3): 1–113.

——1927. *Handbook of the echinoderms of the British Isles*. 471 pp. Oxford University Press, London.

—— 1928. *A monograph of the Echinoidea* Vol. I. Cidaroidea. 551 pp. C. A. Reitzel, Copenhagen.

—— 1935. *A monograph of the Echinoidea* Vol. II. Bothriocidaroida, Melonechinoida, Lepidocentroida & Stirodonta. 647 pp. C. A. Reitzel, Copenhagen.

—— 1943. *A monograph of the Echinoidea* Vol. III(3). Camarodonta. 2. Echinidae, Strongylocentrotidae, Parasaleniidae, Echinometridae. 446 pp. C. A. Reitzel, Copenhagen.

—— 1950. *A monograph of the Echinoidea* Vol. V(1). Spatangoida 1. 432 pp. C. A. Reitzel, Copenhagen.

—— 1951. *A monograph of the Echinoidea* Vol. V(2). Spatangoida 2. Amphisternata. 2. Spatangidae, Loveniidae, Pericosmidae, Schizasteridae, Brissidae. 593 pp. C. A. Reitzel, Copenhagen.

Nichols, D. 1959. Changes in the chalk heart-urchin *Micraster* interpreted in relation to living forms. *Phil. Trans. R. Soc. B* **242:** 347–437.

Ohshima, H. 1911. Note on a gigantic form of Auricularia allied to *A. nudibranchiata* Chun. *Annotnes zool. jap.* **7:** 347–352.

—— 1915. Report on the holothurians collected by the *Albatross* in the northwestern Pacific. *Proc. U.S. natn. Mus.* **48:** 213–291.

Östergren, H. 1905. Zwei koreanische Holothurien. *Archs Zool. exp. gén.* (4)**3,** Notes et Revue No. 8: cxcii–cxcix.

Pawson, D. L. 1965. The bathyal holothurians of the New Zealand region. *Zoology Publs. Vict. Univ. Wellington* **39:** 1–33.

—— 1969. Holothuroidea from Chile. Report No. 46 of the Lund University Chile Expedition 1948–1949. *Sarsia* **38:** 121–145.

—— 1971. Second New Zealand record of the holothurian giant larva *Auricularia nudibranchiata* Chun. *N.Z. Jl mar. freshw. Res.* **5:** 381–387.

—— 1976. Some aspects of the biology of deep-sea echinoderms. *Thalassia jugosl.* **12**(1): 287–293.

—— 1982. Deep-sea echinoderms in the Tongue of the Ocean, Bahama Islands: a survey, using the research submersible *Alvin*. *Mem. Aust. Mus.* No. 16: 129–145.

—— **& Fell, H. B.** 1965. A revised classification of the dendrochirote holothurians. *Breviora* No. 214: 1–7.

Pequegnat, W. E., James, B. M., Bouma, A. H., Bryant, W. R. & Fredericks, A. D. 1972. Photographic study of the deep-sea environment of the Gulf of Mexico. pp. 67–128. *In:* Texas, A. & M. University: Oceanographic Studies Vol. 3.

—— **& Jeffrey, L. M.** 1979. Petroleum in deep benthic ecosystems of the Gulf of Mexico and Caribbean Sea. *Contr. mar. Sci.* **22:** 63–75.

Péquignat, C. E. 1970. Biologie des *Echinocardium cordatum* (Pennant) de la Baie de Seine *Forma et Functio* **2:** 121–168.

Perrier, R. 1902. Holothuries. *Expéd. scient. Travailleur Talisman* **5:** 273–554.

Phelan, T. 1970. A field guide to the cidaroid echinoids of the northwestern Atlantic Ocean, Gulf of Mexico, and the Caribbean Sea. *Smithson. Contr. Zool.* No. 40: 1–67.

Prouho, H. 1888. Recherches sur le *Dorocidaris papillata,* et quelques autres Échinides de la Méditerranée. *Arch. Zool. exp. gén.* (2)**5:** 213–380.

Rice, A. L., Aldred, R. G., Billett, D. S. M. & Thurston, M. H. 1979. The combined use of an epibenthic sledge and a deep-sea camera to give quantitative relevance to macro-benthos samples. *Ambio Spec. Rept.* **6:** 59–72.

Roberts, D. G. 1975. Marine geology of the Rockall Plateau and Trough. *Phil. Trans. R. Soc.* **A278:** 447–509.

Roe, H. S. J. & Shale, D. M. 1979. A new multiple rectangular midwater trawl (RMT 1+8 M) and some modifications to the Institute of Oceanographic Sciences' RMT 1+8. *Mar. Biol.* **50:** 283–288.

Rowe, F. W. E. & Pawson, D. L. 1967. A new genus in the holothurian family Synaptidae, with a new species from Tasmania. *Rap. Proc. R. Soc. Tasm.* **101:** 31–35.

Rowe, G. T. 1971. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. *Deep-Sea Res.* **18:** 569–581.

—— **& Menzies, R. J.** 1969. Zonation of large benthic invertebrates in the deep sea off the Carolinas. *Deep-Sea Res.* **16:** 531–537.

Sanders, H. L. 1979. Evolutionary ecology and life-history patterns in the deep sea. *Sarsia* **64:** 1–7.

Sars, M. 1868. Om nogle Echinodermer og Coelenterater funde ved Lofoten. [In Norwegian]. *Forh. Vidensk Selsk. Krist.* **1867:** 19–23.

Semon, R. 1888. Die Entwickling der Echinodermen. *Jena Z. Naturw.* **22:** 175–309.

Shearer, C., Morgan, W. de & Fuchs, H. M. 1914. On the experimental hybridization of echinoids. *Phil. Trans. R. Soc.* B **204:** 255–362.

Sibuet, M. 1974. *Cherbonniera utriculus* gen. nov., sp. nov., petite Holothurie (Molpadonia, Molpadiidae) des vases abyssales du Nord-Est Atlantique. *C.r. hebd. Seanc. Acad. Sci., Paris* (D) **279:** 1443–1445.

—— 1977. Repartition et diversité des Echinodermes (Holothurides-Astérides) en zone profonde dans le Golfe de Gascogne. *Deep-Sea Res.* **24:** 549–563.

—— **& Lawrence, J. M.** 1981. Organic content and biomass of abyssal holothuroids (Echinodermata) from the Bay of Biscay. *Mar. Biol.* **65:** 143–147.

——**, Khripounoff, A., Deming, J., Colwell, R. & Dinet, A.** 1982. Modification of the gut contents in the digestive tract of abyssal holothurians. pp. 421–428. *In:* Lawrence, J. M. [Ed.] *Echinoderms: Proceedings of the International Conference, Tampa Bay.* A. A. Balkema, Rotterdam.

Smith, A. B. 1980*a*. The structure, function, and evolution of tube feet and ambulacral pores in irregular echinoids. *Palaeontology* **23**(1): 39–83.

—— 1980*b*. The structure and arrangement of echinoid tubercles. *Phil. Trans. R. Soc.* **289**(1033): 1–54.

—— 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology* **24**(4): 779–801.

Southward, A. J., Robinson, S. G., Nicholson, D. & Perry, T. J. 1976. An improved stereocamera and control system for close-up photography of the fauna of the continental slope and outer shelf. *J. mar. biol. Ass. U.K.* **56:** 247–257.

Théel, H. 1882. Report on the Holothurioidea dredged by H.M.S. Challenger during the years 1873–1876. Part 1. *Rep. scient. Results Voy. Challenger* (Zool.) **4**(13) 1–176.

—— 1886*a*. Report on the Holothurioidea dredged by H.M.S. Challenger during the years 1873–1876. Part 2. *Rep. scient. Results Voy. Challenger* (Zool.) **14**(39): 1–290.

—— 1886*b*. Report on the Holothuridae of the 'Blake' expedition. *Bull. Mus. comp. Zool. Harv.* **13**(1): 1–21.

Thomson, C. W. 1874. On the Echinoidea of the 'Porcupine' deep-sea dredging-expeditions. *Phil. Trans. R. Soc.* **164**(2): 719–756.

Tyler, P. A. & Gage, J. D. 1983. The reproductive biology of *Ypsilothuria talismani* (Holothuroidea: Dendrochirota) from the N.E. Atlantic. *J. mar. biol. Ass. U.K.* **63:** 609–616.

—— **&** —— 1984*a*. Seasonal reproduction of *Echinus affinis* (Echinodermata: Echinoidea) in the Rockall Trough, NE Atlantic Ocean. *Deep-Sea Res.* **31:** 387–402.

—— **&** —— 1984*b*. The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, NE Atlantic). *Mar. Biol.* **80:** 63–74.

——, **Grant, A., Pain, S. L. & Gage, J. D.** 1982. Is annual reproduction in deep-sea echinoderms a response to variability in their environment? *Nature* **300:** 747–750.

Tyler, P. A., Muirhead, A., Gage, J. D. & Billett, D. S. M. (in press). Gametogenic strategies in deep-sea echinoids and holothurians from the N.E. Atlantic. *In:* Keegan, B. F. & O'Connor, B. [Eds] *Proc. int. Conf. Echinoderms, Galway, 1984*. Balkema, Rotterdam.

Wesenburg-Lund, E. 1941. Notes on Polychaeta. 1. *Vidensk. Meddr. dansk naturh. Foren.* **105:** 31–48.

Wüst, G. 1936. Schichtung und Zirkulation des Atlantischen Ozeans. Die Stratosphäre des Atlantischen Ozeans. *Wiss. Ergebh. dt. atlant. Exped. 'Meteor'.* **6**(1): 108–288 [English transl. Al-Ahram Center for Scientific Translations, Emergy, W.J. (Ed.) 1978), 112 pp. Amerind, New Delhi].

Manuscript accepted for publication 15 November 1984

Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia) 5. *Palaemon (Palaemon) adspersus* Rathke, 1837

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Introduction

This study on *Palaemon adspersus* completes the descriptive part in the series of papers on the larval development of Palaemoninae found in British waters (Fincham, 1977, 1979*a*, 1979*b*, 1983). *P. adspersus* is widely distributed in shallow water (0–6 m), often in estuarine conditions, and has been recorded from as far north as the Norwegian Sea and the Gulf of Bothnia, to the Bay of Biscay in the south (Fincham & Williamson, 1978). The species is fished commercially in Danish waters (Jensen, 1958), but scarce around the British Isles (Smaldon, 1979). It is with pleasure, therefore, that I thank Dr L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie at Leiden for helping me to collect ovigerous females of *P. adspersus* from a brackish pool in the SW. of the Netherlands, from whence they were transported to the British Museum (Natural History) for rearing. Six larval and the first post larval stages are described in this paper from the laboratory rearing of *P. adspersus*.

Materials and Methods

Ovigerous *Palaemon adspersus* were collected in the SW. of the Netherlands by hand-netting in June 1980 at the edge of an 8 m deep, brackish pool, 'Inlaag 1953', situated just inland from the outer dyke of Schouwen Island (Zeeland Province) near the town of Ouwerkerk.

Similar rearing techniques to those reported previously (Fincham, 1983) were used. Water temperature was maintained at 15°C and salinity of the recirculating water system at 10‰, equivalent to those recorded in Inlaag 1953 at the time of sampling. Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1984.337.

Palaemon (Palaemon) adspersus Rathke, 1837

Cancer squilla Linnaeus, 1758
Palaemon adspersus Rathke, 1837
Palaemon fabricii Rathke, 1843
Palaemon rectirostris Zaddach, 1844
Leander rectirostris Czerniavsky, 1884
Leander adspersus var. *fabricii* De Man, 1915
Palaemon (Palaemon) squilla Holthuis, 1950
Palaemon (Palaemon) adspersus Holthuis, 1957

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. Czerniavsky, 1884. zoea 1, Figs 30, 31 (as *Leander rectirostris*); Mortensen, 1897 zoeae I–V, post larva, Plate 1, Figs 1–3, 5–8, Plates 2, 3, Plate 4, Figs 1, 3–4, plankton (as *Leander fabricii*); Kalichevsky, 1904 (as *Leander rectirostris*); Sollaud, 1923 (as *Leander adspersus*); Makarov & Golodetsky, 1980; zoeae 1–5, post larva, Figs 1–3, laboratory reared.

In the following short descriptions of the key characters of the larval stages, setal counts have been omitted usually but they are recorded in Table 1.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(4): 215–231

Issued 31 October 1985

Table 1 Larval development and range of morphological and meristic variation in *Palaemon adspersus*. R = rudimentary; + = present/yes; − = absent/no; W = wide; N = narrow;[1] reduced setation on exopodite.

	Zoea/Moult						
	1	2	3	4	5	6	PL1
Carapace							
No. dorsal spines	0	1	2	3	3	3	3–5
No. ventral rostral spines	0	0	0	0	0	0	1–2
Supraorbital spines +/−	−	+	+	+	+	+	−
No. antero-lateral spines	0	1	2	2	2	2	2
Rostrum tip—downturned +/−	−	+/−	−	−	−	−	−
Ventral retrorse hooks +/−	+	+	+	−	−	−	−
	One group				Two groups		
Antenna 1							
No. groups aesthetascs	1W,2N	2W,2N	3W	3W,1N	3W,1N 2N	3W,1N 2N	3W 2N
Stylocerite +/−	−	R	+	+	+	+	+
Statocyst +/−	−	−	−	R	R	R	+
No. segments flagellum internal	0	0	0	0	1	1	4
external	1	1	1	1	1	1	3
Accessory flagellum +/−	−	−	−	−	−	−	−
Antenna 2							
Endopodite—No. segments	1	1	3–4	3–4	5–6	7–8	many
Length of scaphocerite	0·68:1 to 0·72:1	0·67:1 to 0·72:1	0·73:1 to 0·80:1	0·90:1 to 0·95:1	⩽	>	>
Exopodite—No. distal segments	5	4–5	3	0	0	0	0
No. plumose setae	9+2	14+2	18+2 to 20+2	21+2 to 22+23	24–26	26–28	⩾30
External spine +/−	−	−	−	−	−	−	+
Mandible—Lacinia mobilis +/−	+	+	+	+	+	+	−
Palp	−	−	−	−	−	−	−
Maxilla 1							
No. endite setae—Coxa	6	6	6	7	7	7	c.8
Basis	5	7	7	8	8	8–9	c.16
Maxilla 2							
No. endite setae—Coxa	4	4	4	4	4	4	0
Basis 1	3	3	3	3	3	3	5
Basis 2	4	4	4	4	4	4	6
Endopodite	3	3	3	3	3	3	0
No. plumose setae—Exopodite	5	7	10–11	13–16	17–19	22–24	c.26
Maxilliped 1							
No. setae on internal margin—Coxa	1	1	1	1	1	1	c.4
Basis	6	6	6	6	8	8	c.22
Exopodite no. setae—Lateral	0	0	0	0	1	3	c.7
Maxilliped 2							
Endopodite—No. of segments	4	4	4	4	4	4	5
Exopodite +/−	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+/−
Maxilliped 3							
Endopodite—No. of segments	4	4	5	5	5	5	5
Exopodite +/−	+	+	+	+	+	+	+
Setae +/−	+	+	+	+	+	+	+/−
Pereiopods 1 & 2 +/−	R	+	+	+	+	+	+
Biramous +/−	+	+	+	+	+	+	+
Endopodite—propodus fixed finger +/−	−	−	−	+	+	+	+
Pereiopod 3 +/−	−	R	R	+	+	+	+
Biramous +/−		+	+	+	+	+	+[1]

continued

Table 1 *Continued.*

	Zoea/Moult						
	1	2	3	4	5	6	PL1
Pereiopod 4 +/−	−	R	R	R	+	+	+
Biramous +/−		+	+	+	+	+	+[1]
Pereiopod 5 +/−	−	R	R	+	+	+	+
Biramous +/−		−	−	−	−	−	−
Abdomen							
Somite 5—lateral spines +/—	−	+	+	+	+	+	+/−
Somite 6—'Continuous' with Telson +/−	+	+	−	−	−	−	−
Pleopods +/−	−	−	−	R	R	R	+
Fringing setae +/−				−	−	−	+
Appendix interna 2–5 +/−				−	−	−	+
Telson							
Posterior margin concave (−)/ convex (+)	+/−	+/−	−	−	−	+/−	+
Spine formula	7+7	7+7	[1]6+ 6[1]	[1]4+ 4[1]	[1]4+ 4[1]	[1]4+ 4[1]	2+2
Small spines +/−	+	+	+	+	+	+	−
No. prs. lateral spines	0	0	0	0	0	0	2
Uropods +/−	−	−	+	+	+	+	+
Long plumose setae—Endopodite			0	9–11	15–17	18–20	23–27
Exopodite			11–12	16–19	19–22	22–24	26–30

Description of larval stages

Key characters are printed in *italic* type and are useful for separating stages in British species.

Zoea 1 (Fig. 1) 2·6 mm (2·5–2·7 mm)

Head (Figs 1a,b): *eyes sessile.*

Carapace (Figs 1a,b): *without spines, rostrum straight,* tapering distally, ventral margin with minute retrorse teeth distally, *shorter than peduncle of antenna 1.*

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, two narrow, one wide.

Antenna 2 (Fig. 1d): peduncle with short spine on inner antero-lateral corner. Exopodite as a broad lamina divided into 5 short segments distally with 9+2 plumose setae on inner and distal margins. Endopodite of one segment (0·7 length of exopodite) with terminal plumose seta and a short spine.

Mandibles (Fig. 1e): assymetrical.

Maxillipeds 1–3 (Figs 1h–j): with natatory exopodites.

Pereiopods 1,2 (Figs 1k,l): *rudimentary, biramous.*

Pereiopods 3–5: absent.

Abdomen (Figs 1a,b): *somite 5 with posterior margin rounded,* not produced into spines, somite six continuous with telson. No trace of pleopods.

Telson (Fig. 1p): fans out distally, posterior margin almost straight, bearing 7+7 spines, with minute spines between four innermost spines.

Zoea 2 (Fig. 2) 2·8 mm (2·7–2·9 mm)

Head (Figs 2a,b): *eyes stalked.*

Carapace (Figs 2a,b): *one dorso-medial and a pair of supra-orbital spines* all bent forward with small retrorse teeth, *rostrum straight with retrorse teeth ventrally at tip.*

Antenna 1 (Fig. 2c): *two peduncle segments, stylocerite forming on proximal external margin of first segment; single flagellar segment with four terminal aesthetascs, two wide and two narrow.*

Antenna 2 (Fig. 2d): exopodite with 5 short segments distally.

Pereiopods 1,2 (Figs 2k,l): *developed with natatory expodite.*

Pereiopods 3,4 (Figs 2m,n): *rudimentary, biramous.*

Pereiopod 5 (Fig. 2o): *rudimentary, uniramous.*

Abdomen (Figs 2a,b): *somite 5 with posterior margin produced into a pair of conspicuous lateral spines; somite 6 continuous with telson.*

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton* alongside telson proper; *in central group of small spines, one pair longer than others.*

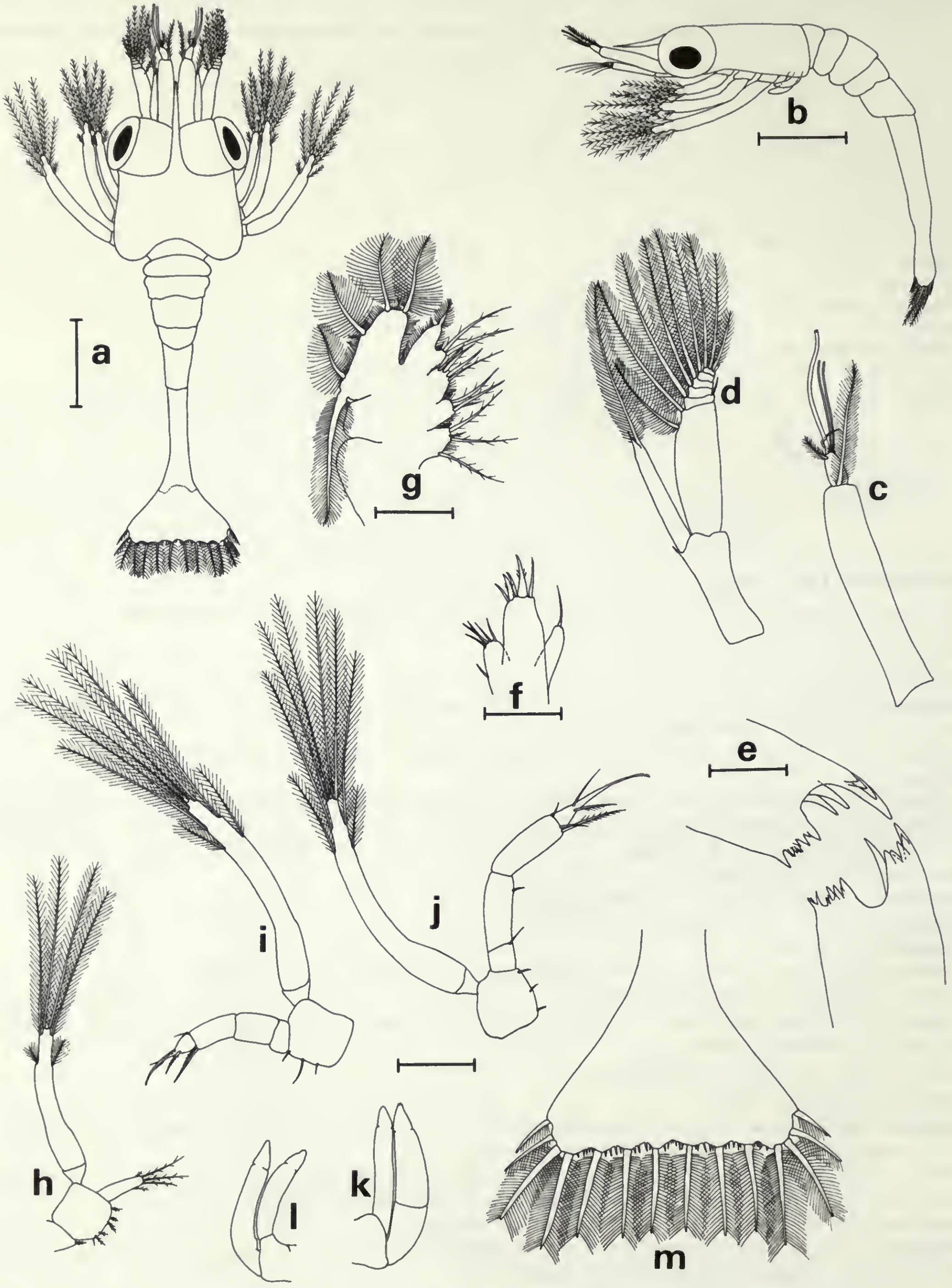

Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a,b = 0·5 mm; c,d, h–m = 0·2 mm; f,g = 0·1 mm; e = 0·05 mm.

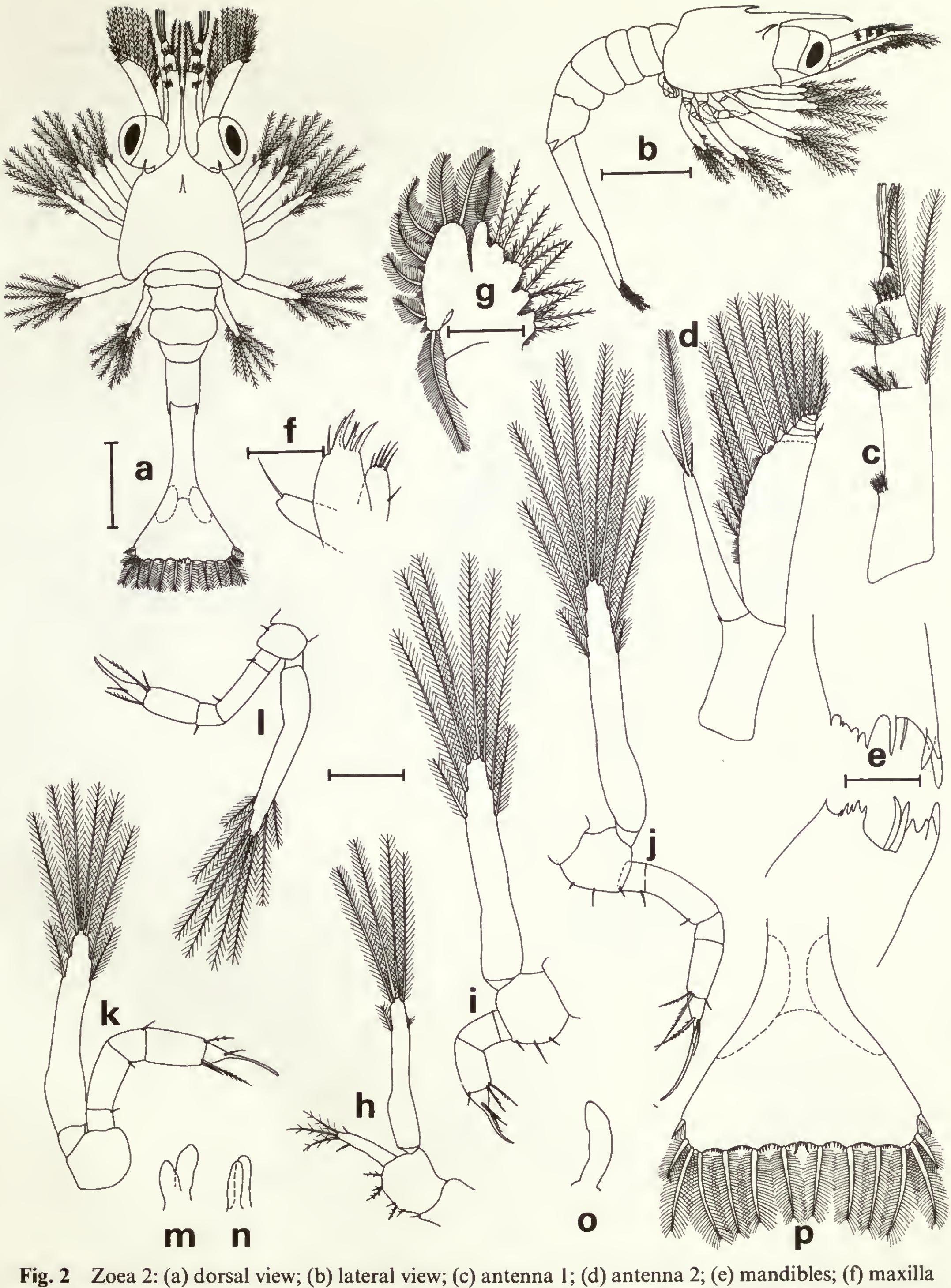

Fig. 2 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a,b = 0·5 mm; c,d,h–p = 0·2 mm; f,g = 0·1 mm; e = 0·05 mm.

Zoea 3 (Figs 3,4) 3·3 mm (3·0–3·8 mm)

Carapace (Figs 3a,b): *two dorso-medial spines* and pair of small fronto-lateral spines at edge of carapace beneath eyes, former with retrorse teeth ventrally; rostrum straight with retrorse teeth ventrally at tip.
Antenna 1 (Fig. 4a): *conspicuous spine medially,* stylocerite more pronounced; distal segment of peduncle bearing *first segment of internal flagellum,* single segment of *external flagellum bearing 3 wide aesthetascs distally.*
Antenna 2 (Fig. 4b): exopodite with distal part divided into 3 short segments, *endopodite of 3 segments.*
Abdomen (Figs 3a,b, 4k): *somite 6 divided from telson by suture. Uropod endopodite rudimentary with no marginal setae, exopodite with marginal setae.*
Telson (Fig. 4k): narrower but still broader distally, outer pair of spines on posterior margin much reduced or absent on one or both sides.

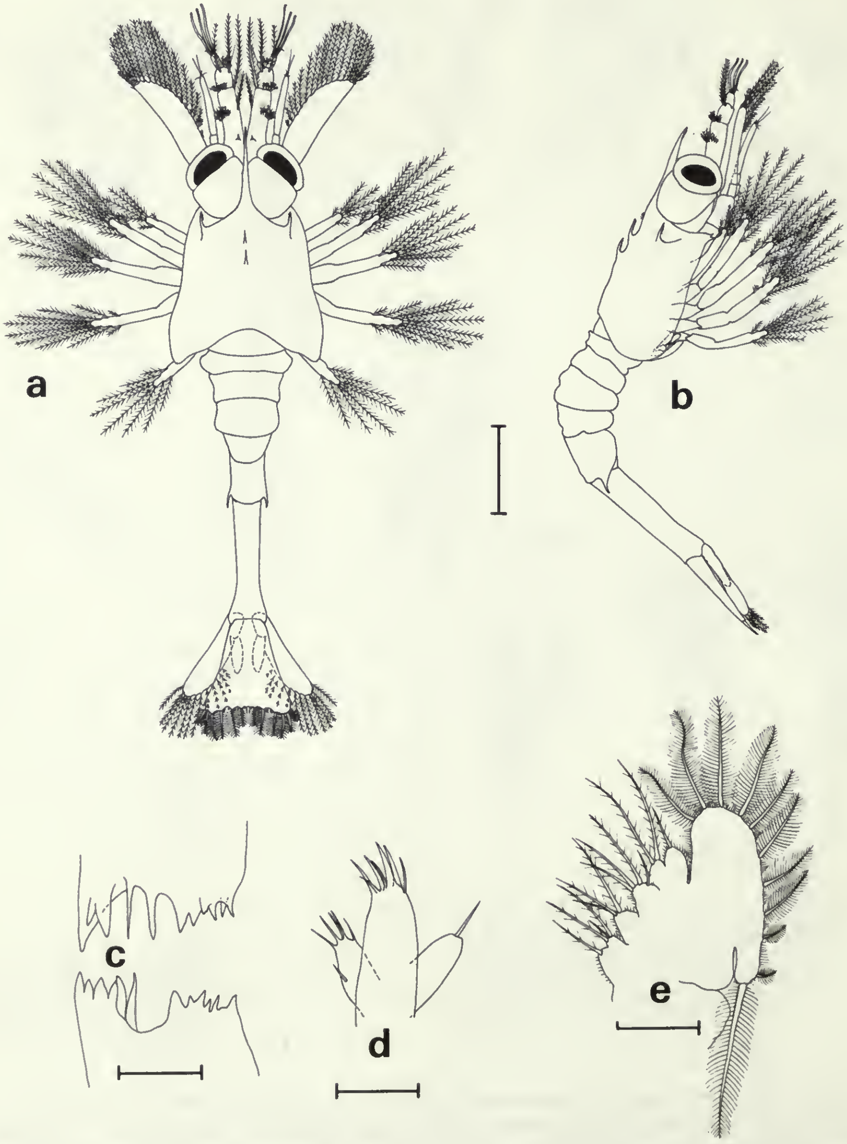

Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a,b = 0·5 mm; c = 0·05 mm; d,e = 0·1 mm.

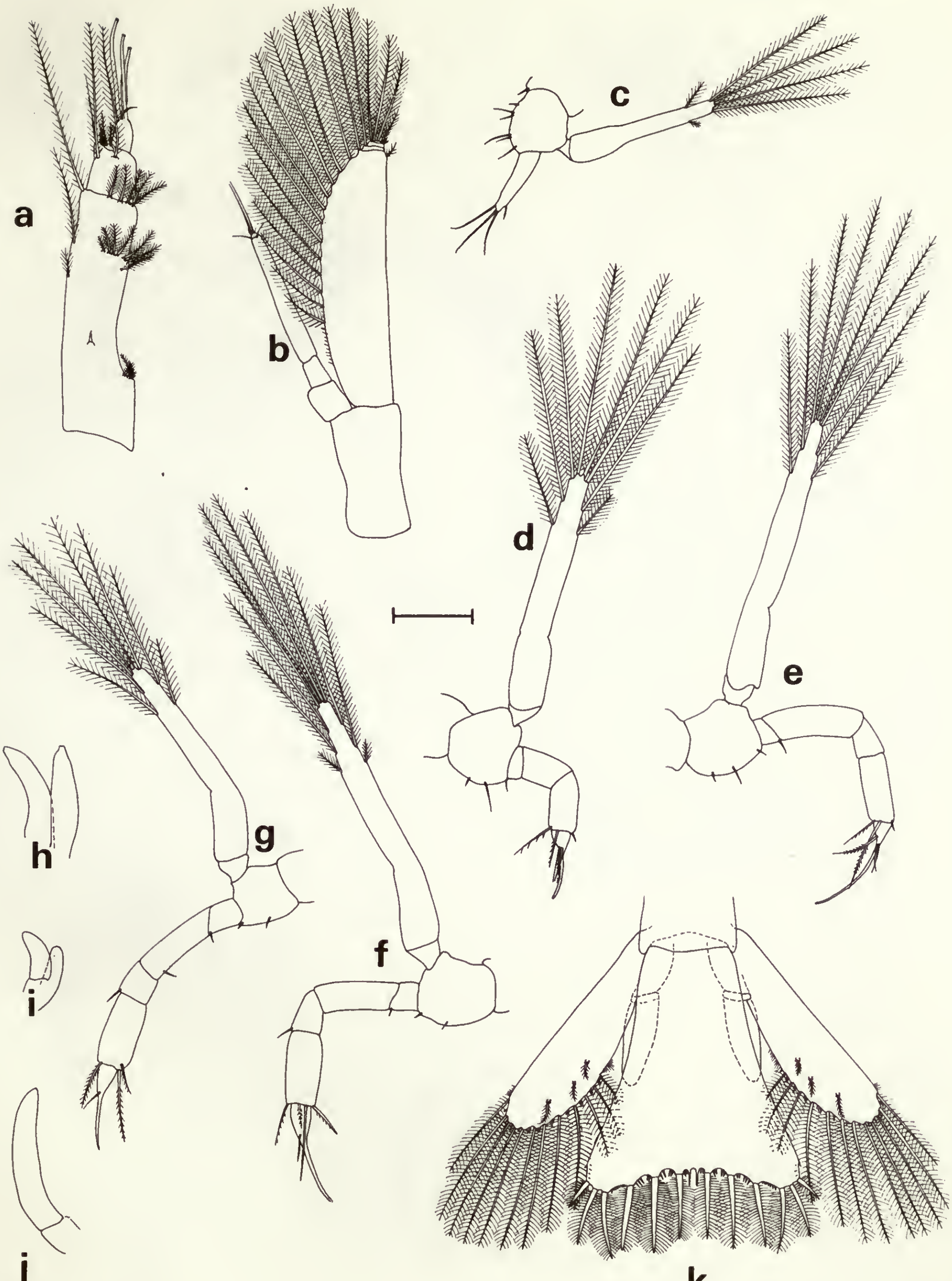

Fig. 4 Zoea 3: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: 0·2 mm.

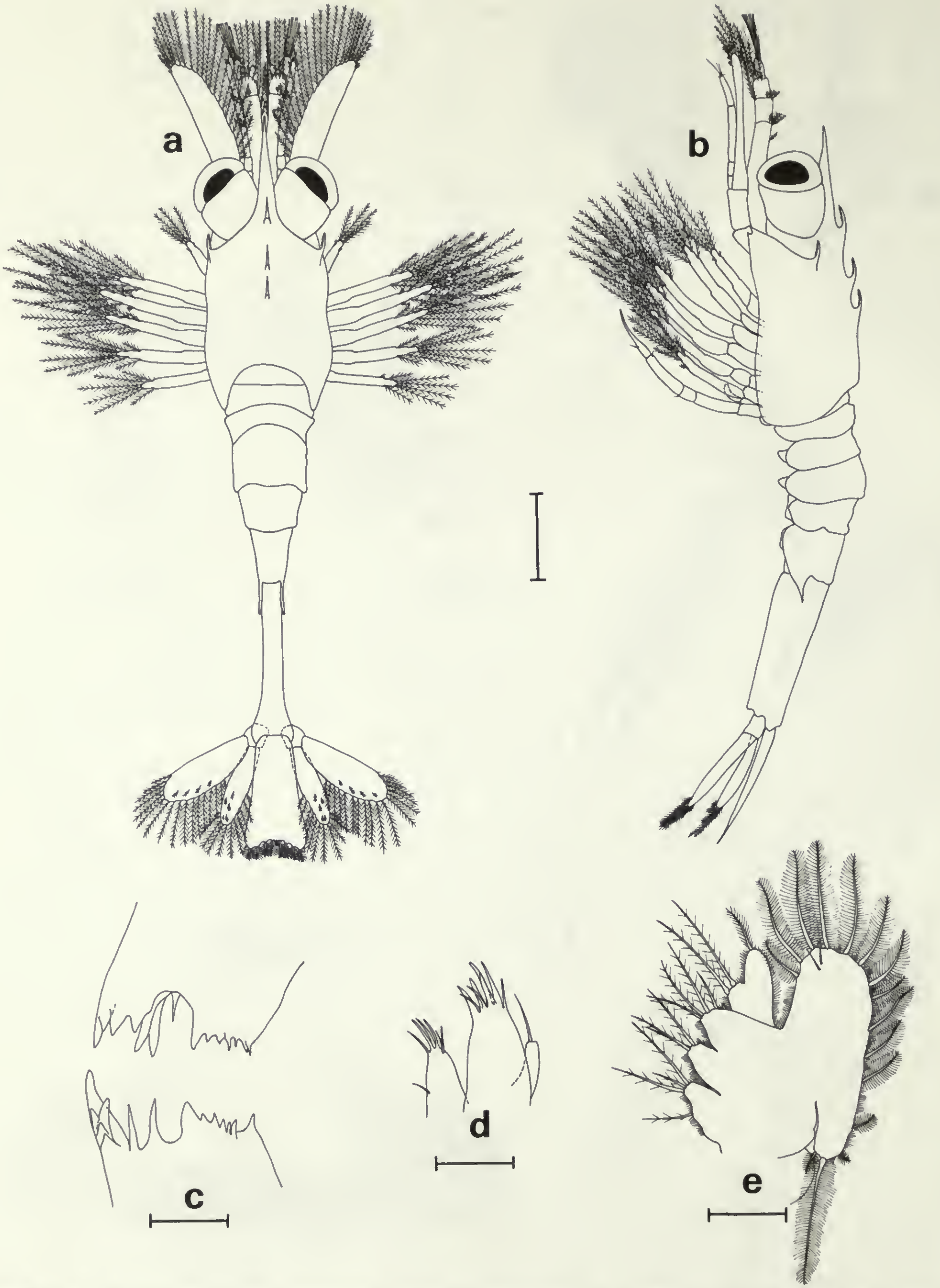

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandibles; (d) maxilla 1; (e) maxilla 2. Bar scales: a,b = 0·5 mm; c = 0·05 mm; d,e = 0·1 mm.

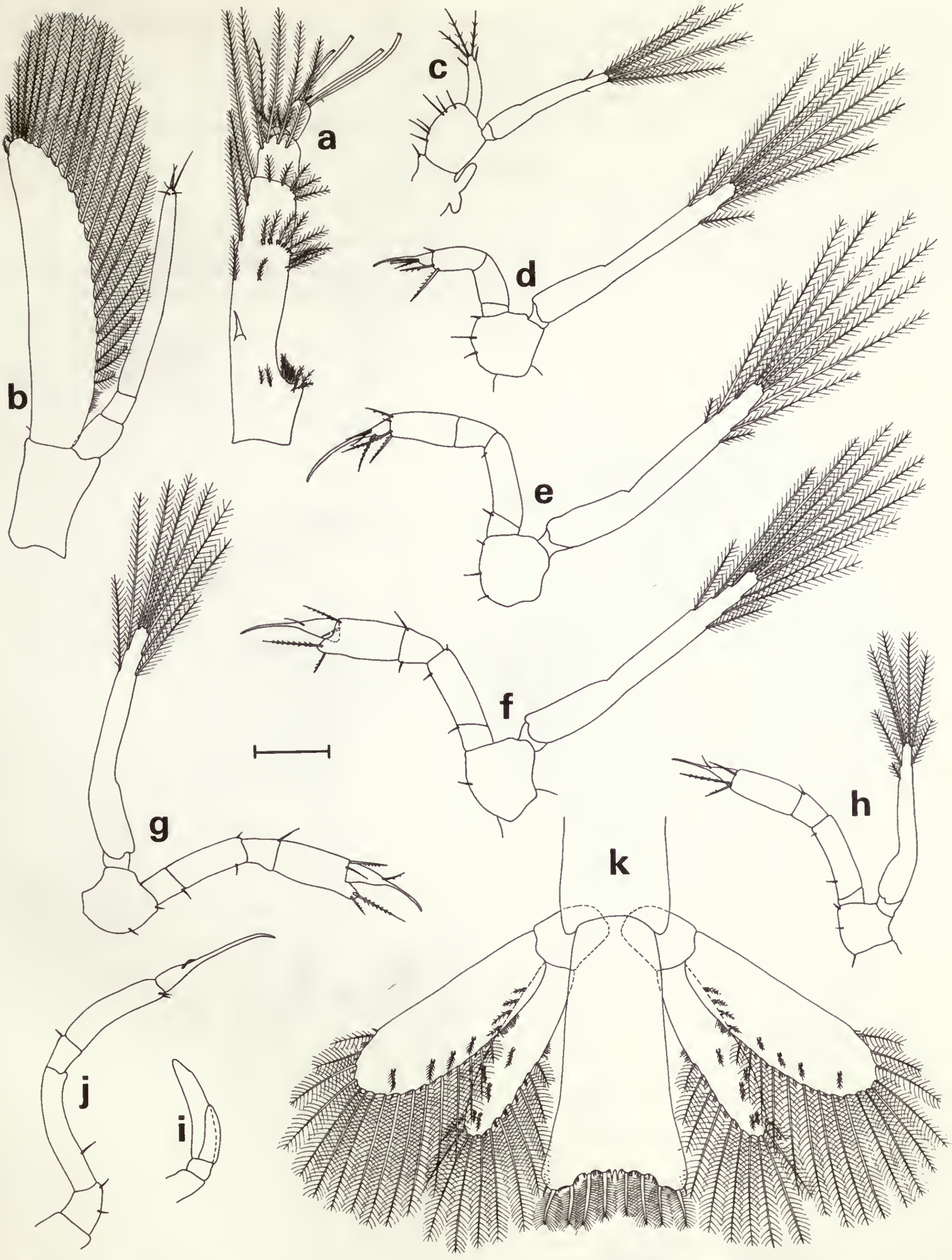

Fig. 6 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: 0·2 mm.

ZOEA 4 (Figs 5,6) 4·2 mm (4·0–4·3 mm)

Carapace (Fig. 5a,b): *three dorso-medial spines* with retrorse teeth ventrally; pair of small fronto-lateral teeth at edge of carapace beneath the eyes; *rostrum straight*, but with no retrorse teeth at tip.

Antenna 1 (Fig. 6a): *single segment of external flagellum bearing 3 wide and 1 narrow aesthetascs distally.*

Antenna 2 (Fig. 6b): distal part no longer divided into segments.

Pereiopods 1,2 (Figs 6f,g): *endopodite with internal distal margin of propodus produced slightly forward* (will become fixed finger of chela).

Pereiopod 3 (Fig. 6h): *developed with natatory exopodite.*

Pereiopod 4 (Fig. 6i): *rudimentary, biramous.*

Pereiopod 5 (Fig. 6j): *developed, uniramous.*

Abdomen (Figs 5a,b, 6k): *endopodite and exopodite of uropod both with marginal plumose setae.*

Telson (Fig. 6k): narrower, but still broader distally; posterior margin weakly concave with *4+4 large spines;* latero-distal margin spines reduced to one small pair, or a single spine on one side, or absent.

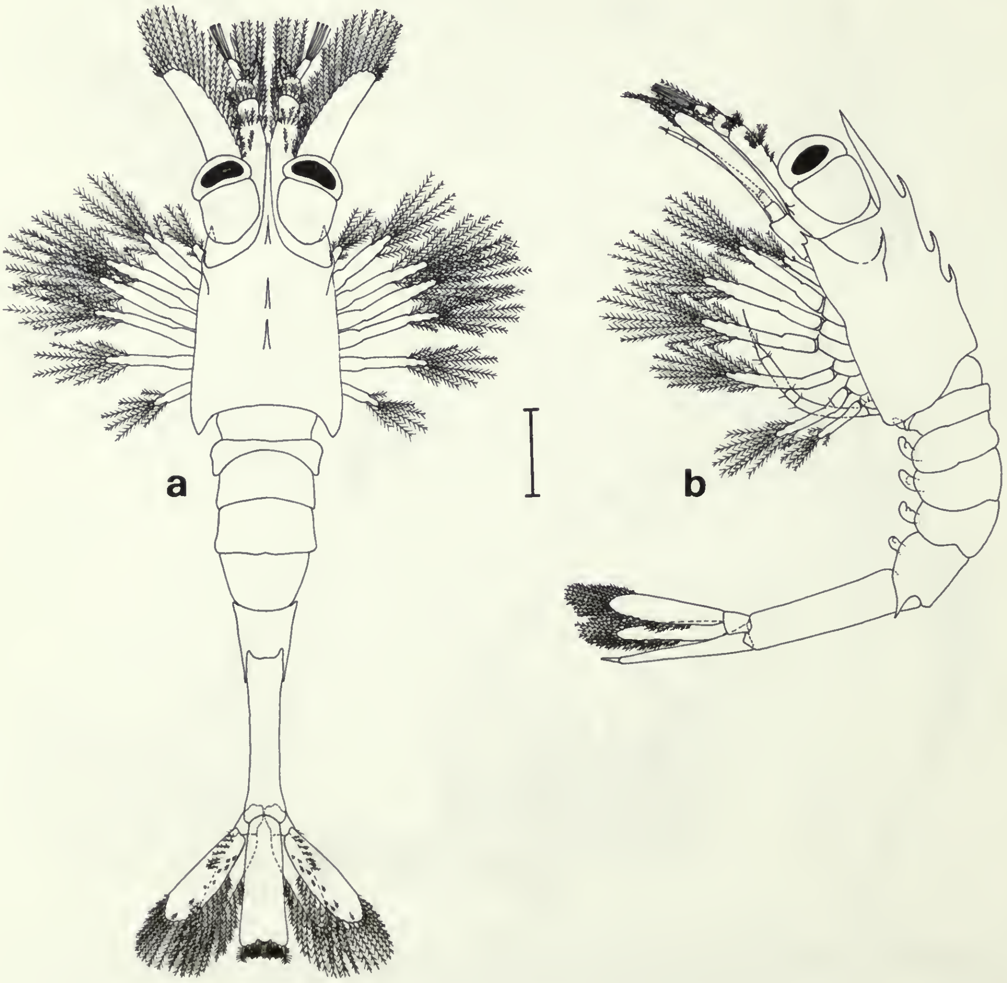

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view. Bar scale: 0·5 mm.

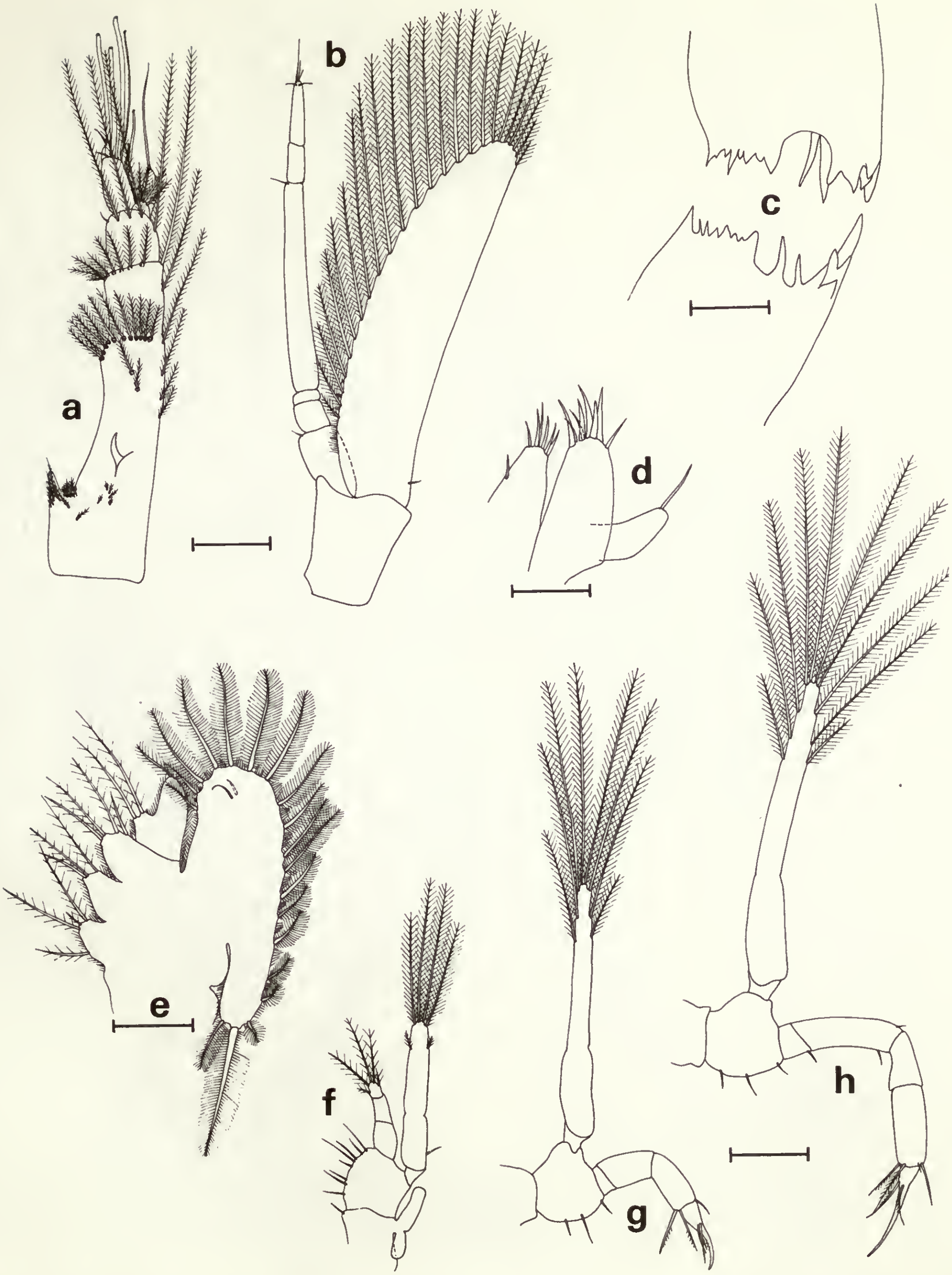

Fig. 8 Zoea 5: (a) antenna 1; (b) antenna 2; (c) mandibles; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2; (h) maxilliped 3. Bar scales: a,b,f–h = 0·2 mm; c = 0·05 mm; d,e = 0·1 mm.

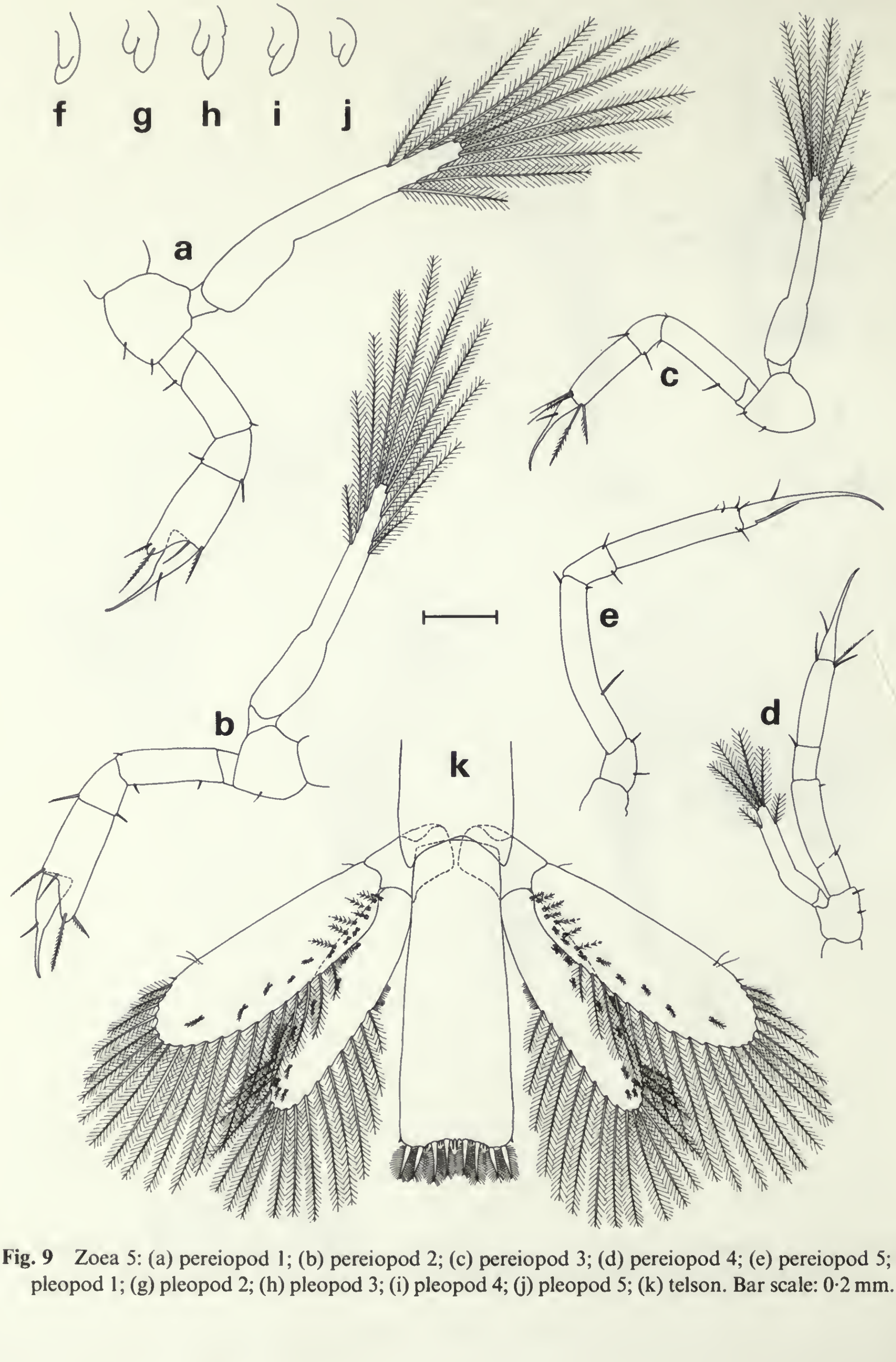

Fig. 9 Zoea 5: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson. Bar scale: 0·2 mm.

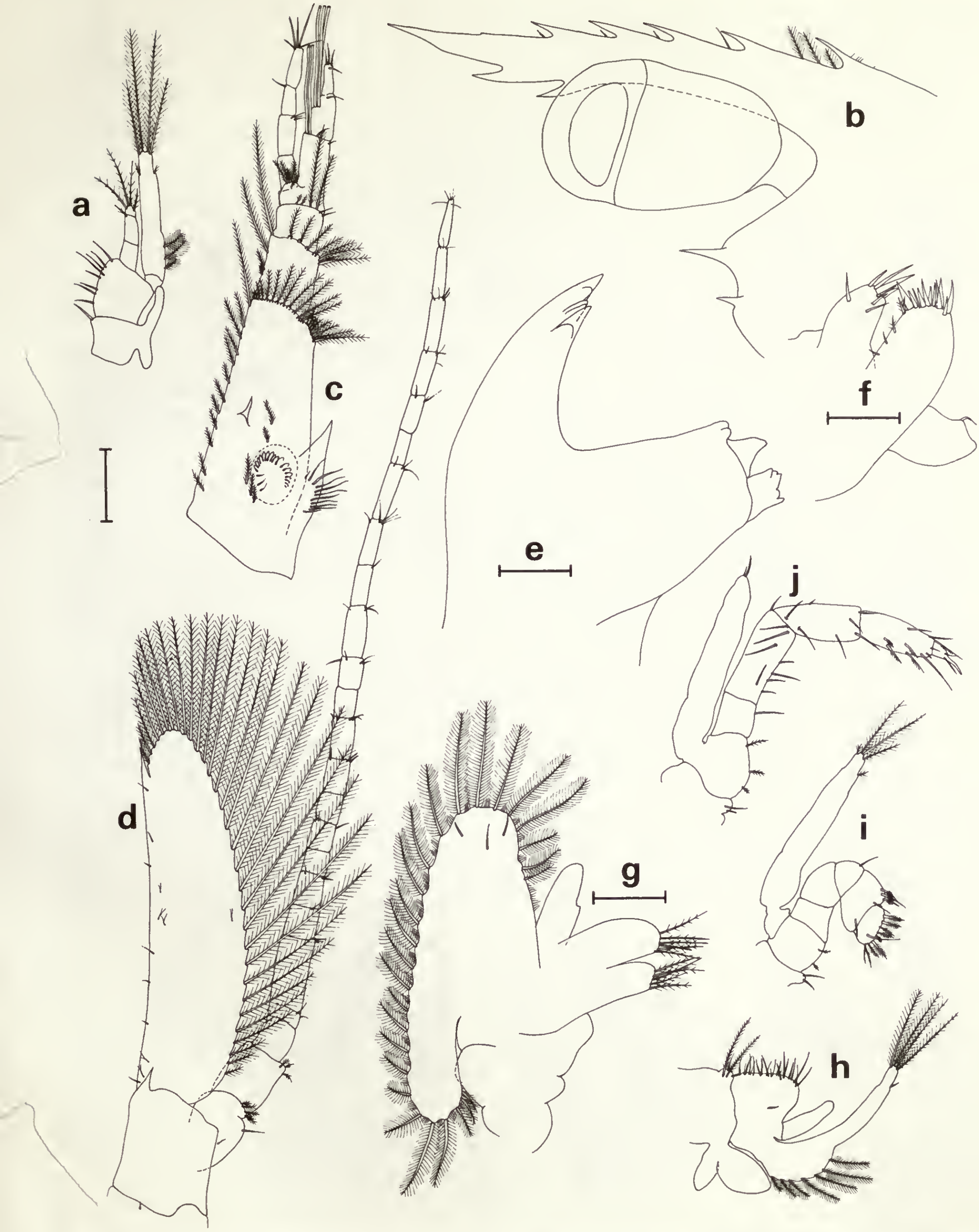

Fig. 10 Zoea 6: (a) maxilliped 1; Post larva 1: (b) rostrum and anterior of carapace; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3. Bar scales: a–d, h–j = 0·2 mm; e = 0·05 mm; f,g = 0·1 mm.

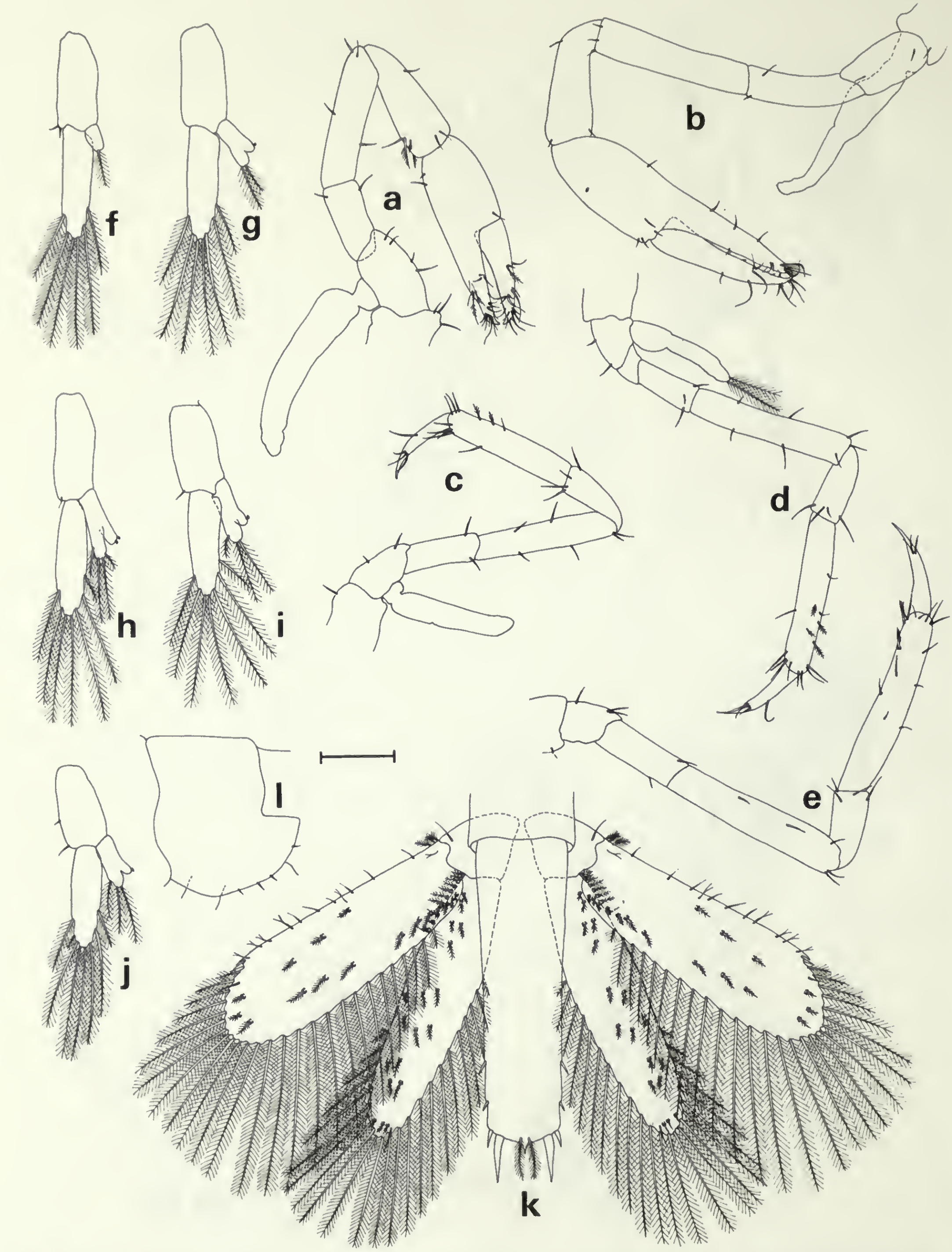

Fig. 11 Post larva 1: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5; (f) pleopod 1; (g) pleopod 2; (h) pleopod 3; (i) pleopod 4; (j) pleopod 5; (k) telson; (l) abdominal somite 5 with weak postero-lateral spine. Bar scale: 0·2 mm.

ZOEA 5 (Figs 7–9) 4·7 mm (4·5–5·0 mm)

Antenna 1 (Fig. 8a): *single segment of external flagellum bearing three wide and one narrow aesthetascs distally, additional group of 2 narrow aesthetascs on internal margin; rudiment of circular statocyst visible on first segment of peduncle.*
Antenna 2 (Fig. 8b): endopodite flagellum of about six segments, *equal to or just longer than scaphocerite in length.*
Maxilliped 1 (Fig. 8f): *8 setae on internal margin of basis,* 0 or 1 plumose seta on proximo-lateral margin of exopodite.
Pereiopods 1,2 (Figs 9a,b): *endopodite with internal distal margin of propodus produced forward to more than half length of dactylus* (excluding narrowed terminal portion).
Pereiopod 4 (Fig. 9d): *developed, exopod with fringing setae.*
Abdomen (Figs 7b, 9f–j): *rudimentary, biramous pleopods on somites 1–5.*

ZOEA 6 (Fig. 10a) 4·7 mm (4·5–5·0 mm)

Maxilliped 1 (Fig. 10a): *3–4 plumose setae on proximo-lateral margin of exopodite.*

POST LARVA 1 (Figs 10,11) 5·0 mm (4·8–5·5 mm)

Most specimens had metamorphosed to post larvae at this moult but a few specimens moulted once more before metamorphosing.
Carapace (Fig. 10b): *rostrum with 3–5 dorsal and 1–2 ventral teeth* (rostral tip straight). *Supra-orbital spines missing.*
Antenna 1 (Fig. 10c): *internal flagellum usually of 4 segments and external flagellum usually of 3 segments.*
Antenna 2 (Fig. 10d): endopodite multisegmented at least twice as long as scaphocerite.
Mandible (Fig. 10e): *divided into pars incisiva and pars molaris*; lacinia mobilis absent and palp (three-jointed in adult) not yet developed.
Maxilla 2 (Fig. 10g): complete loss of setae on coxal endite and endopodite, increase in setae on basal endites.
Maxilliped 1 (Fig. 10h): *six or more plumose setae on proximo-lateral margin of exopodite,* usually complete loss of terminal plumose setae on endopodite.
Maxilliped 2 (Fig. 10i): *endopodite with dactylus, propodus, carpus and merus flattened.*
Maxilliped 3 (Fig. 10j): endopodite dactylus shortened, terminal setae of exopodite much reduced.
Pereiopods 1,2 (Figs 11a,b): *fingers of chelae of equal length.*
Pereiopods 3,4 (Fig. 11c,d): exopodite plumose setae reduced or absent.
Abdomen (Fig. 11l): somite 5 with weak postero-lateral spines.
Pleopod 1 (Fig. 11f): *ratio of endopodite to exopodite 1:4:* endopodite uniramous, bearing single plumose seta distally, exopodite fringed with long plumose setae.
Pleopods 2–5 (Figs 11g–j): endopodite at least one-third length of exopodite, both with long plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hook(s).
Telson (Fig. 11k): *narrower distally than proximally, posterior margin tapering to a point* flanked by pair of plumose setae and two pairs of spines: two further pairs of spines on lateral margins.

Discussion

Of the five species of palaemonid known to occur in the NE. Atlantic, this is the third that occupies a brackish or estuarine habitat, the others being *Palaemonetes varians* (see Fincham 1979*a*) and *Palaemon longirostris* (see Fincham, 1979*b*). Two other NE. Atlantic palaemonids—*Palaemon elegans* and *P. serratus* (see Fincham 1977 and 1983 respectively) live in more saline littoral conditions. This probing of the freshwater habitat by some palaemonids is associated with a reduction in the number of larval stages in their life histories. *Palaemon elegans* and *P. serratus* reared in the laboratory have nine larval stages whereas *P. longirostris* and *Palaemonetes varians* have seven and five respectively, whilst six are reported here for *P. adspersus*.

Holthius (1969) reported that *P. adspersus* was first recorded from the Netherlands in 1960 from the same pool in which the present ovigerous specimens were collected. The pool was created as a result of the severe storms in 1953. A wide breach in the dyke occurred at Ouwerkerk causing extensive flooding on the island of Schouwen. Tidal currents scoured a deep creek and after the dyke was closed in 1954 a brackish pool remained behind the dyke, with salinity stabilizing at about 11‰. It is the only known locality for *P. adspersus* in the Netherlands (Holthuis, 1969; Heerebout, 1974).

This isolated population of *P. adspersus* formed part of a recent study to quantify genetic differentiation and gene flow using electrophoretic data (Berglund & Lagercrantz, 1983). They found that the *P. adspersus* population from 'Inlaag 1953' was genetically distant from other populations tested and more monomorphic with only one variant allele in the 25 loci tested. Berglund & Lagercrantz suggested that this could be explained by 'founder' effects on small populations.

The classic ontogenetic study on *P. adspersus* by Mortensen (1897) was based on specimens from various sites in Denmark. Specimens collected by Berglund & Lagercrantz (1983) from the Danish, non-tidal Limfjord area showed less genetic variability from other Scandinavian and French sites than from the isolated Dutch population. It was particularly instructive, therefore, to compare the larval drawings made by Mortensen with those prepared for this paper.

The correlation is close, but certain differences are apparent. A comparison of sizes at each stage show Mortensen's larvae to be consistently larger: stage 1: 3·0 mm (2·6 mm, present study), stage 2: 3·0 mm (2·6 mm), stage 3: 4·5–5·0 mm (3·3 mm), stage 4: 6·0 mm (4·2 mm), stage 5: 7·0 mm (4·2 mm) and first post larva: 8·0 mm (5·0 mm). Mortensen's stage 6 is already a post larva complete with fully setose pleopods (Fig. III, 7 VI) whereas stage 6 reported here was the last larval stage with non-setose pleopods (Figs 9f–j) and setose thoracic exopods. This insertion of extra moults in palaemonid species reared in the laboratory has been noted previously (Fincham, 1977, 1979*b*, 1983). The exopodite of maxilliped 1 in PL1 in the present study is naked (Fig. 10h); Mortensen records a well-developed plumose hair (Fig. 11, 6 VI). There is still a weak spine on abdominal somite 5 in PL1 in the present study whereas Mortensen draws an entirely rounded postero-lateral margin (Fig. III, 9 VI). Mortensen's figures do not record small outer spines on the telson after stage 2; although variable, they are present on one or both sides in the present material. Some of these phenetic differences were likely to be the result of the isolation of this Dutch population of *Palaemon adspersus.*

The principal aim of the rearing programme was to produce keys for identifying, to species and stage, prawn and shrimp larvae from the plankton. An earlier attempt to produce such a key for NE. Atlantic palaemonids (Fincham & Williamson, 1978) was based in part on published descriptions that frequently proved inadequate. Early palaemonid larvae of the five species are similar and in order to separate them resort was made to a tabular matrix. Even with this cumbersome arrangement not all stages of the various species could be separated. The morphological stages in the life cycles of the five species are now sufficiently documented from specimens reared from positively identified ovigerous females to enable a subfamilial diagnosis of NE. Atlantic larval Palaemoninae to be prepared. This, together with an up-dated key will form the basis of the concluding paper in this series on palaemonid larvae.

References

Berglund, A. & Lagercrantz, U. 1983. Genetic differentiation in populations of two *Palaemon* prawn species at the Atlantic east coast: does gene flow prevent local adaptation? *Mar. Biol.* **77**: 49–57.

Czerniavsky, W. 1884. Crustacea Decapoda Pontica littoralia, Materialia ad Zoographiam Ponticam comparatum. II. *Trans. Soc. Univ. Kharkow.* **13** (supp.): 1–268.

Fincham, A. A. 1977. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 1. Laboratory methods and a review of *Palaemon (Palaeander) elegans* Rathke, 1837. *Bull. Br. Mus. nat. Hist.* (Zool.) **31** (1): 1–28.

—— 1979*a*. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 2. *Palaemonetes (Palaemonetes) varians* (Leach, 1814) and morphological variation. *Bull. Br. Mus. nat. Hist.* (Zool.) **35** (2): 163–182.

—— 1979*b*. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 3. *Palaemon (Palaemon) longirostris* H. Milne Edwards, 1837 and the effect of antibiotic on morphogenesis. *Bull. Br. Mus. nat. Hist.* (Zool.) **37** (1): 17–46.

—— 1983. Larval development of British prawns and shrimps (Crustacea: Decapoda: Natantia). 4. *Palaemon (Palaemon) serratus* (Pennant, 1777) and functional morphology of swimming. *Bull. Br. Mus. nat. Hist.* (Zool.) **44** (2): 125–161.

Fincham, A. A. & Williamson, D. I. 1978. Crustacea, Decapoda: Larvae. VI Caridea, Families Palaemonidae and Processidae. *Fich. Ident. Zooplancton* **159/160:** 8pp.

Heerebout, G. R. 1974. Distribution and ecology of the Decapoda Natantia of the estuarine region of the rivers Rhine, Meuse and Scheldt. *Neth. J. Sea. Res.* **8** (1): 73–93.

Holthuis, L. B. 1950. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species. 1. Subfamily Palaemoninae. *Siboga Exped.* **39a:** 1–268.

—— 1957. Proposed use of the plenary powers (a) to suppress the specific name *'squilla'* Linnaeus, 1758, as published in the combination *'Cancer squilla'*, and (b) substitute the name *'Palaemon adspersus'* Rathke, 1837, as the name to be cited as that of the type species of the genus *'Palaemon'* Weber, 1795 (Class Crustacea, Order Decapoda). *Bull. zool. Nomencl.* **13**(5): 142–153.

——1969. Enkele interessante Nederlandse Crustacea. *Zool. Bijd.* No. 11: 34–48.

Jensen, J. P. 1958. Studies in the life history of the prawn *Leander adspersus* (Rathke) and the Danish fishery on this species. *Meddr Danm. Fisk. og Havsunders.* **18:** 1–28.

Kalischevsky, M. 1904. The development of *Palaemon rectirostis. Zap. novoross. Obshch. Estest.* **25:** 134–138 (in Russian).

Linnaeus, C. 1758. *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* (Ed. 10) **1:** 1–824.

Makarov, Y. N. & Golodetsky, L. A. 1980. Larval development of the Black Sea prawn *Palaemon adspersus* (Crustacea, Decapoda) in the laboratory. *Zool. Zh.* **59** (3): 375–382 (in Russian, English summary).

Man, J. B. De 1915. On some European species of the genus *Leander* Desm., also a contribution to the fauna of Dutch waters. *Tijdschr. ned. dierk. Vereen.* Ser. 2, **14:** 115–179.

Mortensen, T. 1897. Undersogelser over vor almindelige rejes (*Palaemon fabricii* Rtk.) Biologi og Udviklingshistoire samt Bemaerkninger om rejefiskeriet i de Danske farvande. *Vidensk. Undersog. Fisk. omr. Udg. dansk. Fiskerifor.* **1:** 1–79.

Rathke, H. 1837. Zur Fauna der Krym. Ein Beitrag. *Mem. Acad. Sci St Petersb.* Ser 6B, **3:** 291–454.

—— 1843. Beitrage zur Fauna Norwegens. *Nova Acta Leopoldina* **12:** 6.

Smaldon, G. 1979. *British coastal shrimps and prawns.* Linnaean Society Synopses of the British Fauna, No. 15, Academic Press, London, 126pp.

Sollaud, E. 1923. Le developpement larvaire des Palaemoninae. *Bull. biol. Fr. Belg.* **57:** 509–603.

Zaddach, E. G. 1844. *Synopseos Crustaceorum Prussicorum Prodromus.* Regiomonti. 39pp.

Manuscript accepted for publication 17 December 1984

Larval development of the Mud Crab *Panopeus occidentalis* de Saussure, from Bermuda (Crustacea: Xanthoidea: Panopeidae)

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Introduction

Over 30 species of xanthid crabs have been reported from the waters of Bermuda (see Markham & McDermott, 1981: 1273) but the larval stages of only fourteen have been partly or completely described to date (see Table 1). Of the three *Panopeus* species, larval descriptions are available for *P. bermudensis* Benedict & Rathbun and *P. herbstii* H. Milne Edwards; the account of *P. occidentalis* is unpublished (Kurata, 1970) and may not be of this species but of *Hexapanopeus angustifrons* Benedict & Rathbun (see Martin *et al.,* 1984).

During a 1983 September–October visit to Bermuda the author collected an ovigerous specimen of *Panopeus occidentalis*. This was transported to the larval rearing laboratory in the British Museum (Natural History) and the larvae that hatched were reared to megalopal stage. The complete larval development of *P. occidentalis* is described from this material and the stages are compared with the account given by Costlow & Bookhout (1961*b*) of the larval development of *P. herbstii.*

Adults and juveniles of *P. occidentalis* are similar to those of *P. herbstii.* Rathbun (1930: 334) designated subspecies for both, but the subspecific status is now generally not recognised (Williams, 1965: 197, 198). Specimens of *Panopeus* collected on the shores of St George's Island, Bermuda, were provisionally identified on location by their distinctive colour patterns. Identifications were later confirmed using Rathbun (1930), Williams (1965) and from comparisons with specimens of *P. occidentalis* from Florida and *P. herbstii* from North Carolina in the BM(NH) Collections. The colour of Bermuda specimens of *P. occidentalis* varied from yellow-ochre to a mottled brown and with bands of brown on the walking legs, whereas *P. herbstii* had an overall greenish-brown colour with darker chelipeds and paler walking legs. One diagnostic feature of *P. herbstii* is the continuation of the dark colour, from the propodal prolongation of the chelipeds, onto the outer palmar surface; this feature was apparent only in the largest specimens collected. Verrill (1908: 353) reported *P. occidentalis* as 'not common in Bermuda'. During the present visit both species were found to be more or less equally represented on the mud flats at Ferry Reach, although the larger specimens of *P. occidentalis* and the small ovigerous female (18·0 mm c.l.) was collected from burrows on the lowest part of the shore during low tide.

Material and Methods

The ovigerous female from which the larvae were reared was collected from a mud flat burrow on the lowest part of the shore exposed at low tide in the St David's Road region of Ferry Reach, Bermuda on 29 September 1983. Larvae were reared using methods and apparatus described by Rice & Ingle (1975: 104). Material was fixed in 5% formalin and later transferred to 70% IMS. Drawings and measurements were made with the aid of a *camera lucida* and using a Wild M20 microscope; details of setation were confirmed using interference contrast on an Olympus BH2 microscope. The material has been incorporated in the Collections of the British Museum (Natural History), accession number: 1984: 239, 240.

Bull. Br. Mus. nat. Hist. (Zool.) **48**(4): 233–248

Issued 31 October 1985

The eggs hatched on 5.10.1983 and the first megalops appeared on 14.11.1983; rearing was carried out at temperatures of 22–24°C.

Measurements: T.T. = distance between tips of dorsal and rostral spines; C.L. = carapace length from between the eyes to the posterio-lateral margin.

Descriptions

Panopeus occidentalis de Saussure, 1857

non *Panopeus occidentalis:* Kurata, 1970 (= *Hexapanopeus angustifrons* Benedict & Rathbun)

FIRST ZOEA

Dimensions: T.T. 1–1·1 mm, C.L. 0·4–0·5 mm.
Carapace (Fig. 1a): Dorsal spine evenly curved, stout proximally; rostral spine slightly curved, as long as dorsal spine; lateral spines short and stout; dorso-median elevation prominent; anterio-median setules absent, a small pair of posterio-median setules present (see inset to fig.); posterio-lateral margin of carapace somewhat truncate and with very minute denticles (see inset).
Eyes: Partly fused to carapace.
Antennule (Fig. 1e): Unsegmented, with 3 terminal aesthetascs and one long seta.
Antenna (Fig. 1i): Spinous process long, with a small proximal dorsal spinule; distal half of process with many spines; exopod very small, narrowing distally, with 2 terminal setae (see inset).
Mandible: Incisor and molar processes differentiated.
Maxillule (Fig. 4a): Endopod 2-segmented, with 1,6 setae; basal endite with 5 spines/setae, coxal with 8 spines/setae.
Maxilla (Fig. 4e): Endopod 2-lobed, outer larger than inner slightly stepped and with 5 setae (3 + 2), inner lobe with 3 setae; basal endite 2-lobed, with 4 + 5 setae; coxal endite 2-lobed with 4 + 4 setae; scaphognathite with 3 long plumose setae and a stout plumose posterior projection.
First maxilliped (Fig. 4f): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented, 5th segment shorter than 4th, segments with 3,2,1,2,4 + 1 setae respectively; exopod incipiently 2-segmented, with 4 terminal plumose setae.
Second maxilliped (Fig. 4g): Basis with 4 setae; endopod 3-segmented, with 1,1,4 + 1 setae respectively; exopod incipiently 2-segmented, with 4 terminal plumose setae.
Third maxilliped: Not developed.
Pereiopods: Not developed.
Abdomen (Fig. 2a,3a): 5 segments + telson; 2nd segment with a pair of sub-acute, anteriorly directed, dorso-lateral processes; 3rd segment with a pair of small, acute, posteriorly directed, dorso-lateral processes; posterio-lateral margins of 1st and 2nd segments rounded, 2nd with minute spinules (see inset, fig. 3a), 3rd–5th each extended into an acute process; posterio-dorsal surface of 2nd–5th segments each with a small pair of setules near margin; posterior margins of segments 2–5 with very minute denticles (see inset, fig. 2a). Telson forks slightly diverging distally, each with one prominent dorsal spine and one small and one large lateral spine, forks minutely denticulate proximally (lower inset, fig. 2a); posterior margin of telson with 6 long seta.

SECOND ZOEA

Dimensions: T.T. 1·4–1·5 mm, C.L. 0·6–0·7 mm.
Carapace (Fig. 1b): with 3 pairs of anterio-median setules (see inset); posterio-median setules longer than those of first zoea; posterio-lateral margin of carapace with 1–2 setules (see inset); dorsal margin with pronounced elevation; submedian lobes of rostral base angular.
Eyes: Now free.
Antennule (Fig. 1f): With 4 aesthetascs and one seta.
Antenna (Fig. 1j): Spinous process with some long spines; proximal dorsal spinule very minute, absent in some specimens, exopod with only one terminal setule.
Mandible: unchanged.
Maxillule (Fig. 4b): Endopod setation unchanged; outer margin of basal endite with a plumose seta, distal margin with 8 spines/setae; setation of coxal endite unchanged.
Maxilla (Fig. 5c): Endopod, basal and coxal setation unchanged; scaphognathite with 10 long plumose setae.
First maxilliped: Setation of basis and of endopod unchanged; exopod with 6 terminal plumose setae.

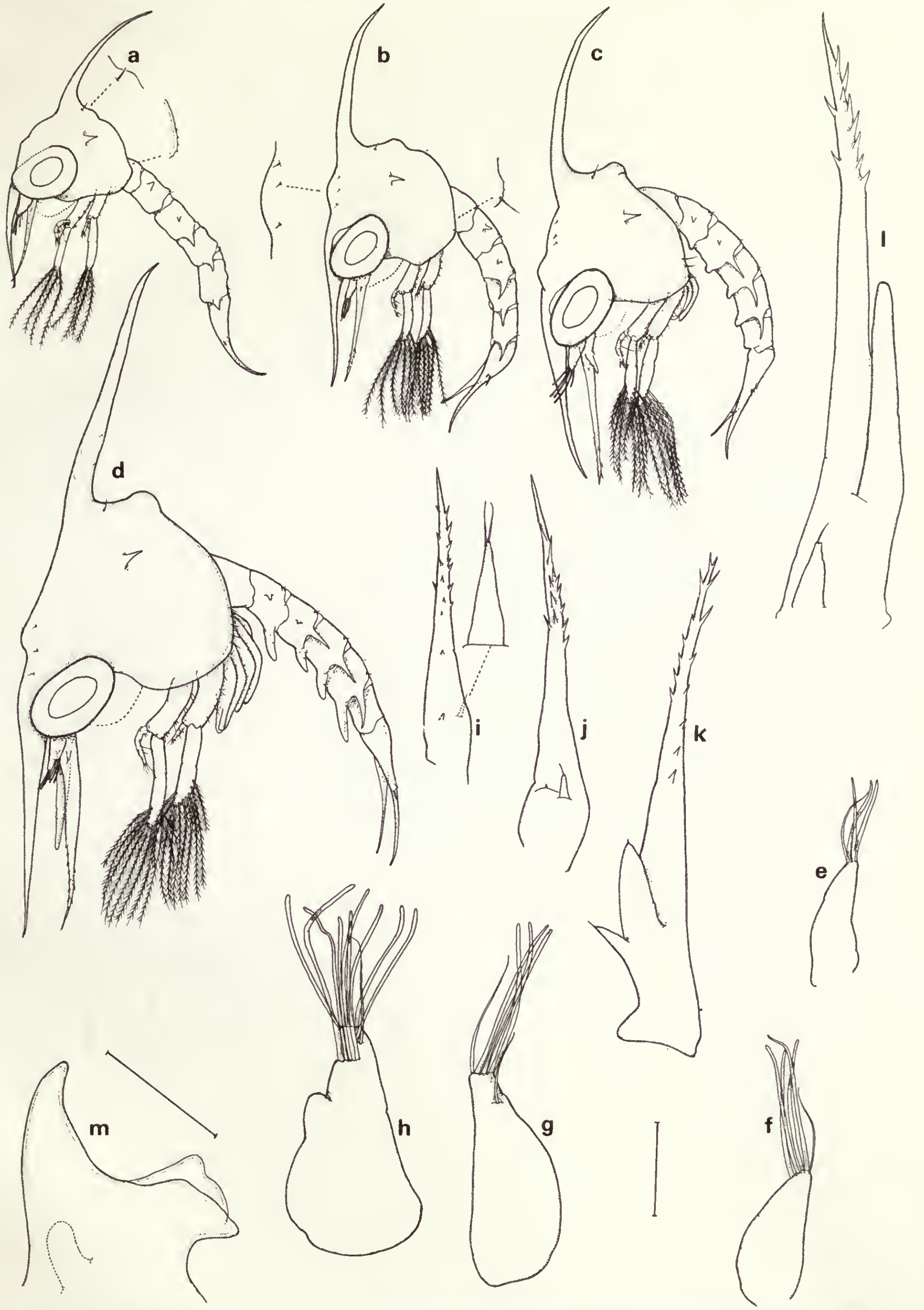

Fig. 1 *Panopeus occidentalis* de Saussure: a–d 1st–4th zoeae from lateral aspects; e–h antennule and i–l antenna of 1st–4th zoeae respectively; m right mandible of 4th zoea; scales = 0·1 mm.

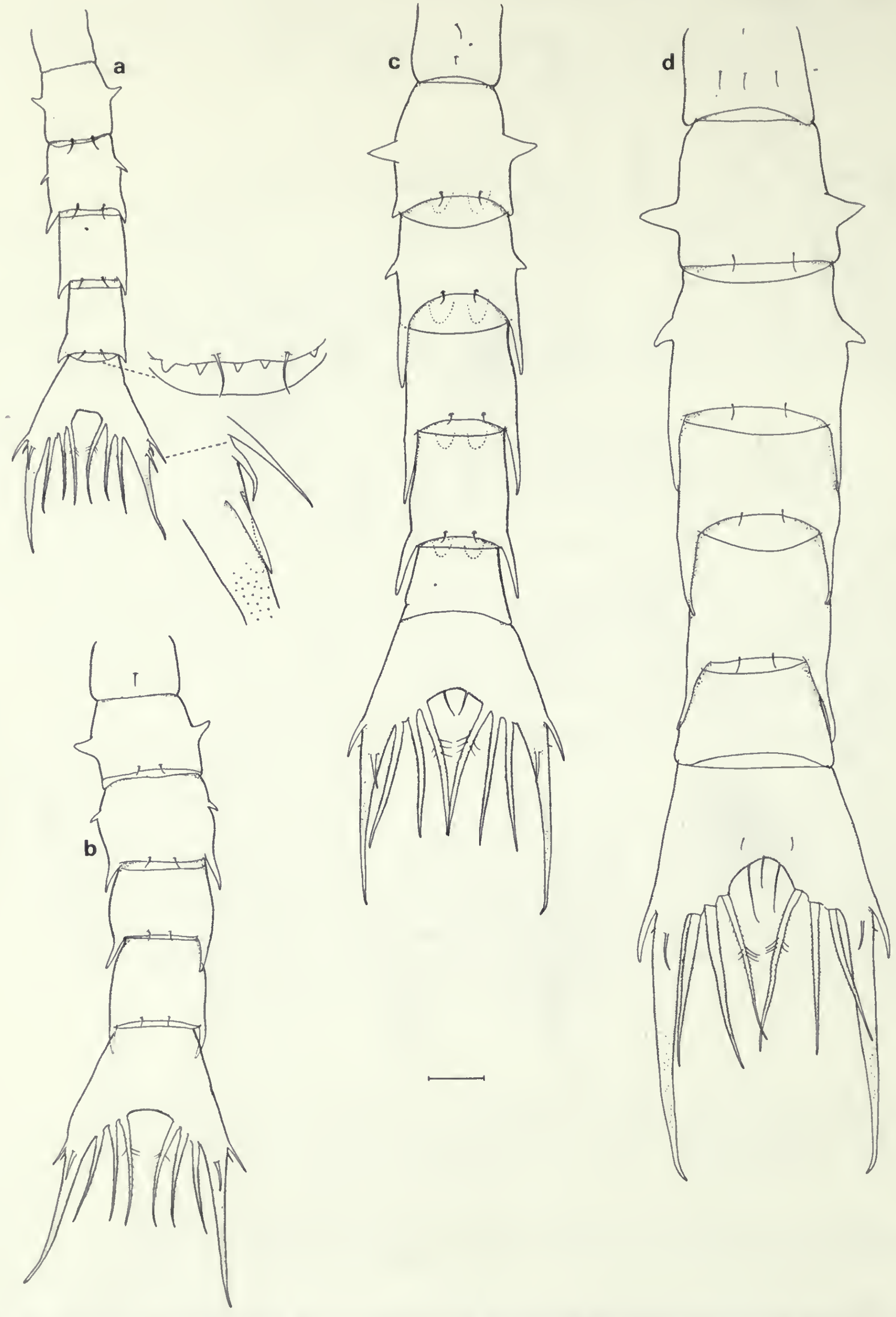

Fig. 2 *Panopeus occidentalis* de Saussure: abdomen and telson from dorsal aspects, a–d of 1st–4th zoeae respectively; scale = 0·1 mm.

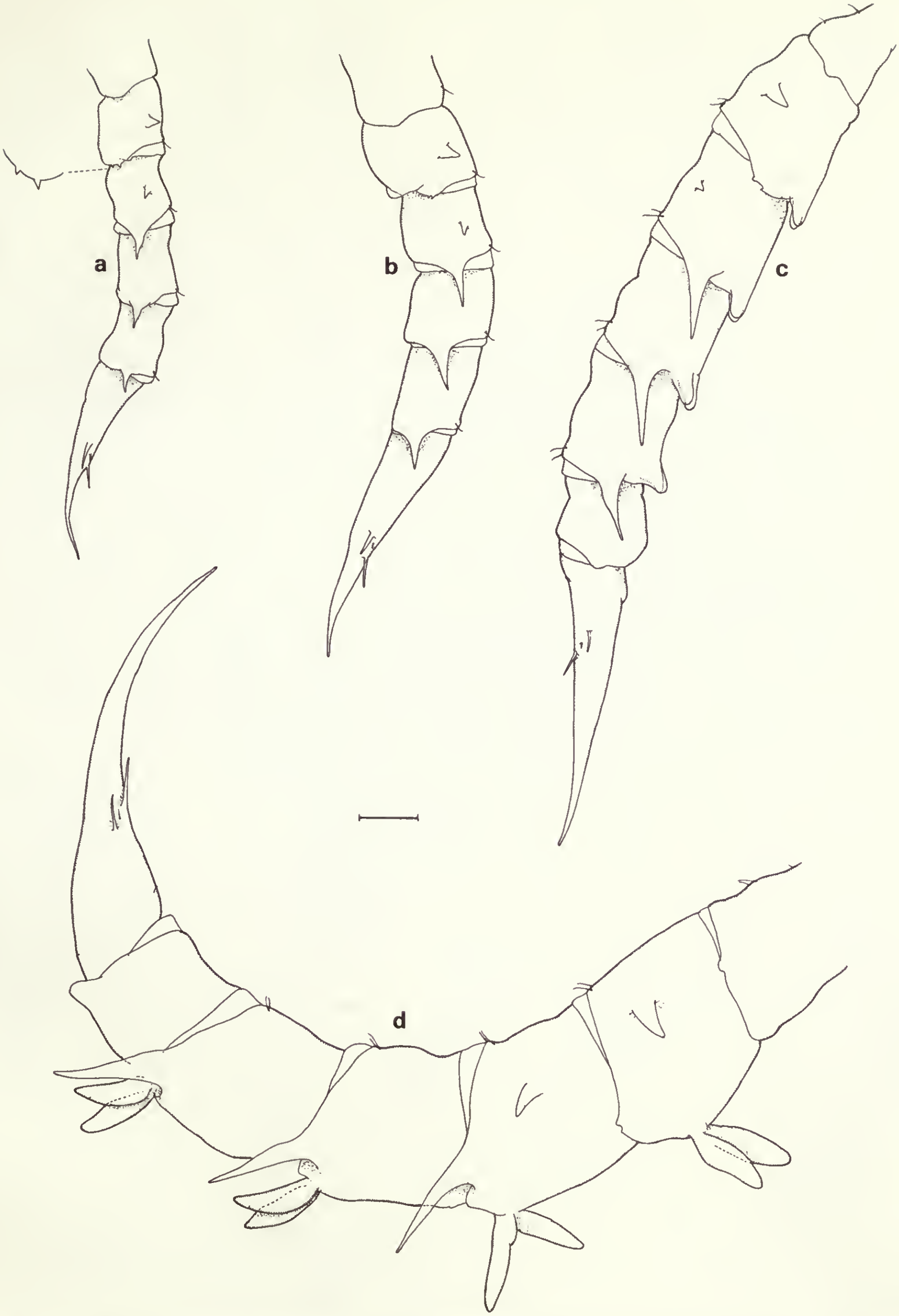

Fig. 3 *Panopeus occidentalis* de Saussure: abdomen and telson from lateral aspects, a–d of 1st–4th zoeae respectively: scale = 0·1 mm.

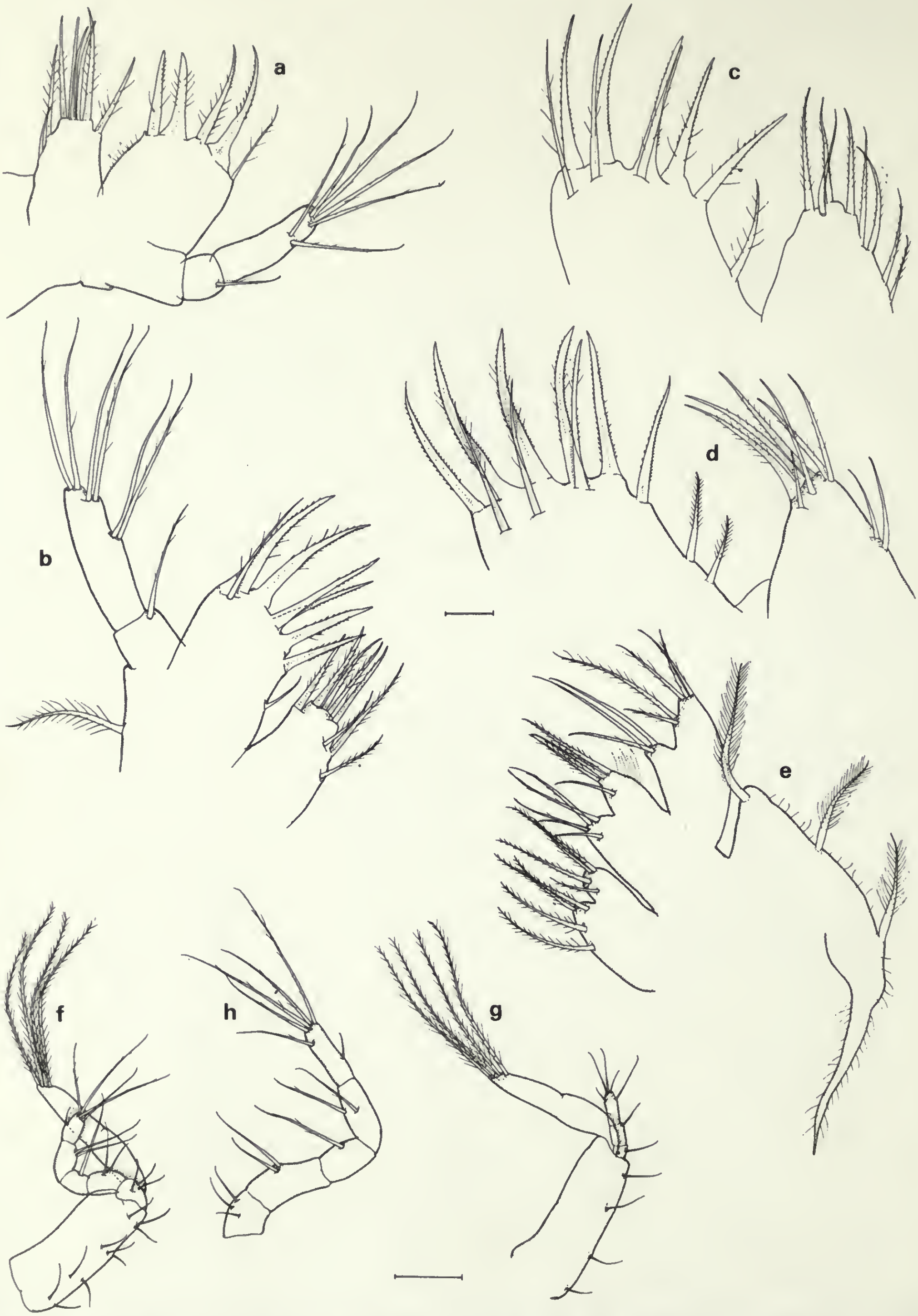

Fig. 4 *Panopeus occidentalis* de Saussure: maxillule a–d of 1st–4th zoeae respectively; e maxilla of 1st zoea, scale = 0·02 mm; f, g 1st and 2nd maxilliped of 1st zoea; h 1st maxilliped endopod of 3rd zoea; scale = 0·1 mm.

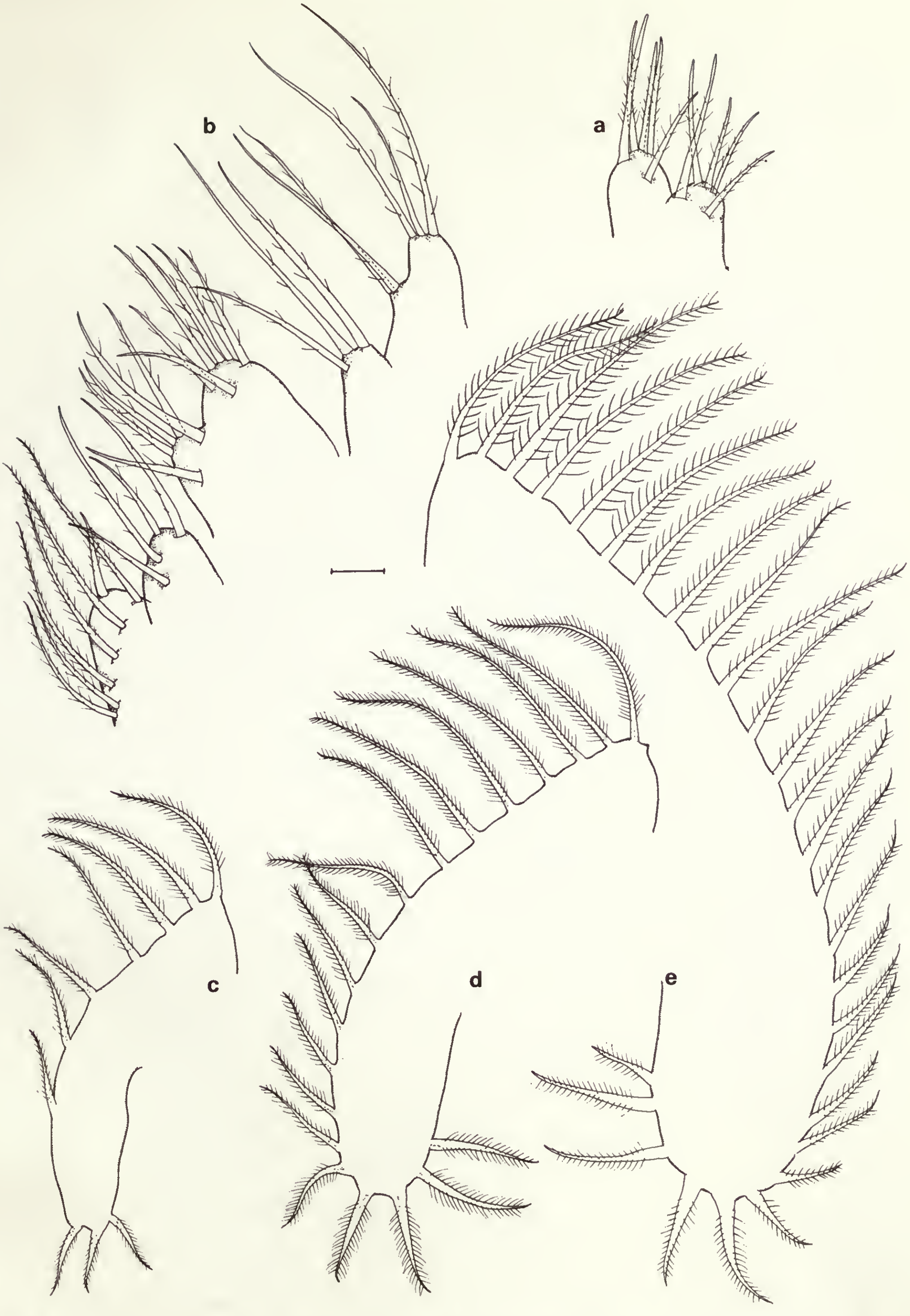

Fig. 5 *Panopeus occidentalis* de Saussure: a maxilla basal endite of 3rd zoea; b maxilla distal endopod, basal and coxal endites of 4th zoeae; maxilla scaphognathite c–e of 2nd–4th zoeae respectively; scale = 0·02 mm.

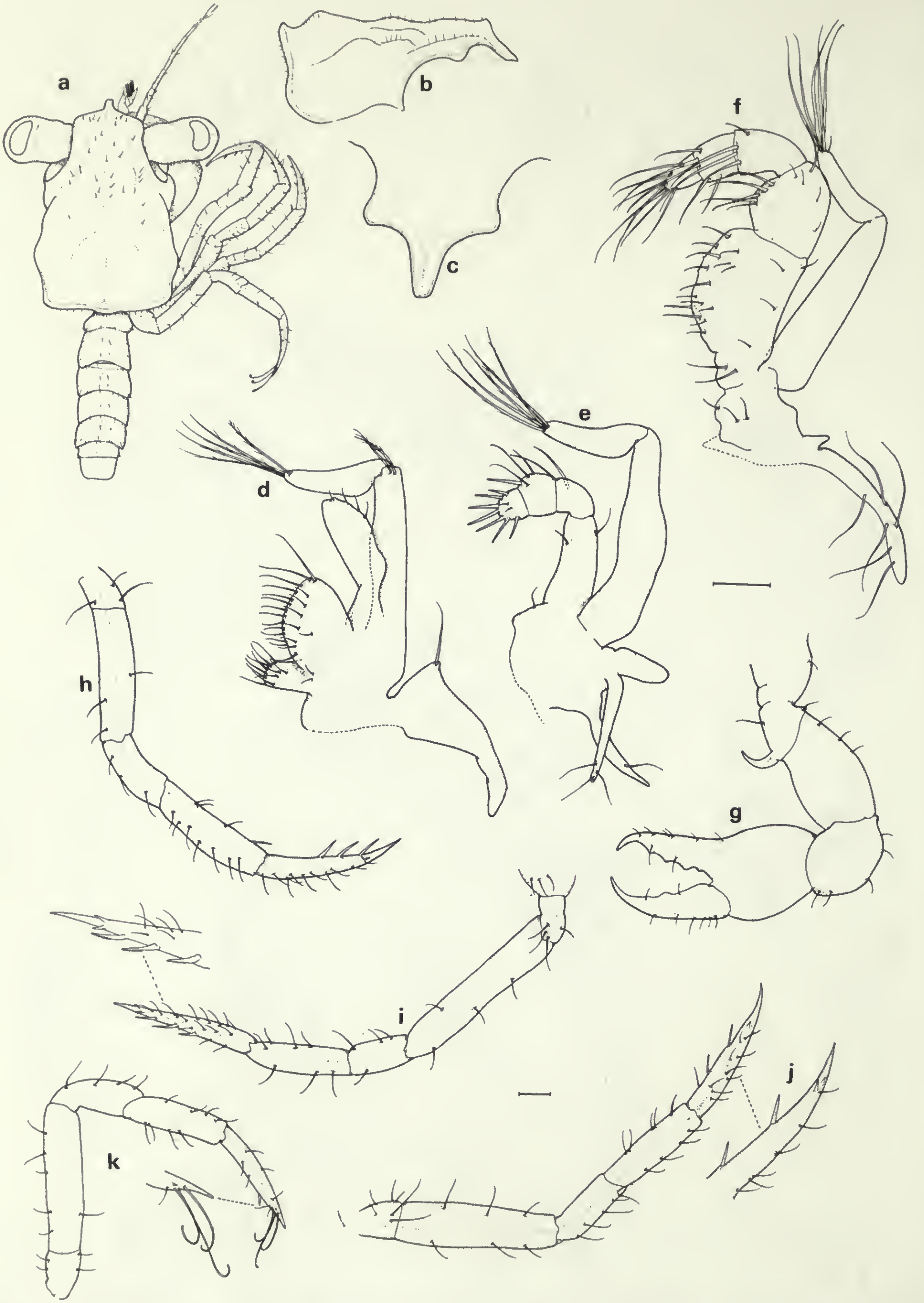

Fig. 6 *Panopeus occidentalis* de Saussure; megalopa—a from dorsal aspect; b carapace from lateral aspect; c rostrum from frontal aspect; d–f 1st–3rd maxillipeds respectively, scale = 0·1 mm; g–k 1st–5th pereiopods respectively, scale = 0·1 mm.

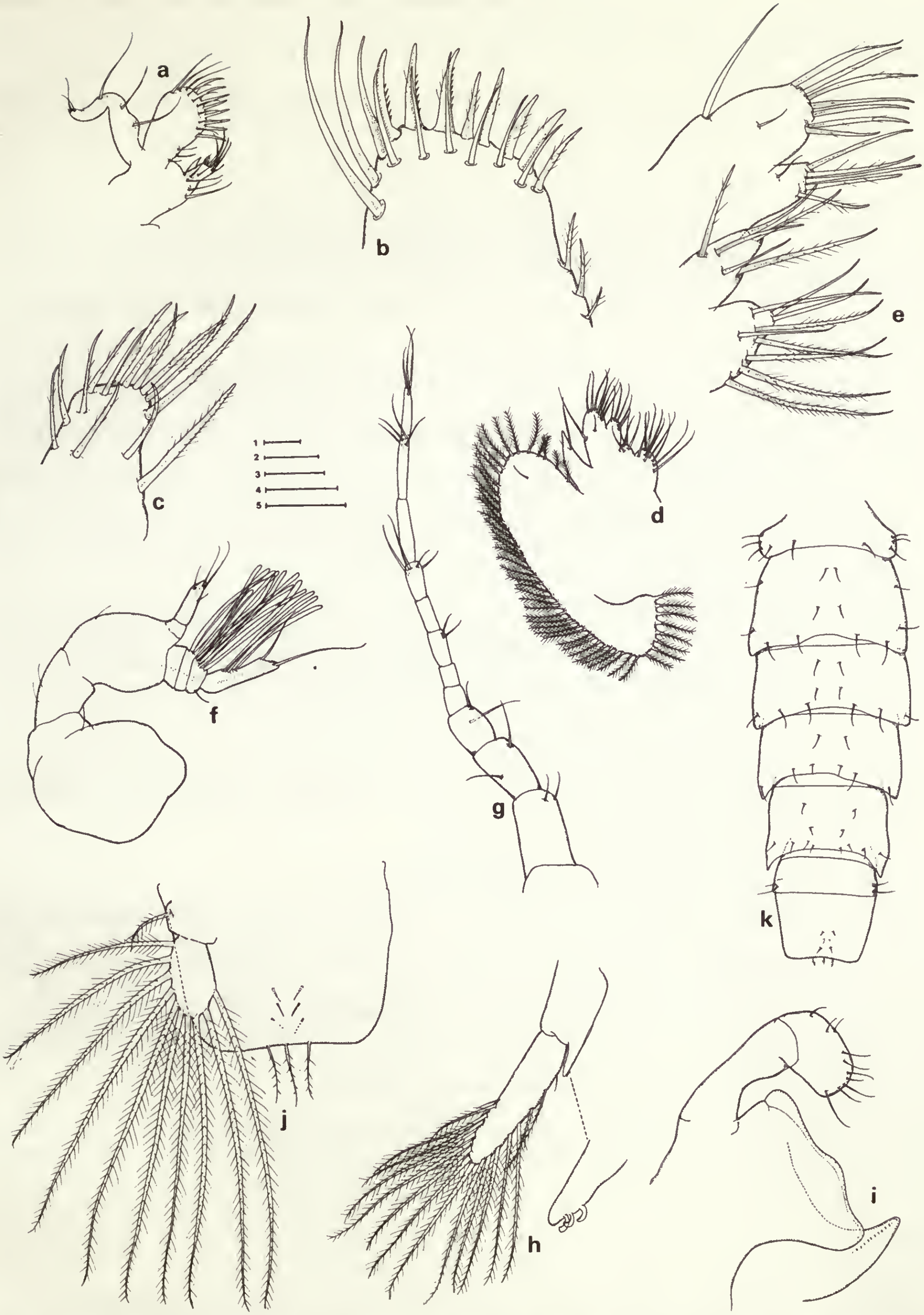

Fig. 7 *Panopeus occidentalis* de Saussure: megalopa—a maxillule; b basal and c coxal endites of maxillule; d maxilla; e basal and coxal endites of maxilla; f antennule; g antenna; h 1st pleopod; i right mandible; j telson and right uropod (ventral aspect); k abdomen from dorsal aspect; scales k to scale 1 = 0·1 mm. b,c,e to scale 2 = 0·02 mm; a,d,f,g to scale 3 = 0·1 mm; h,j to scale 5 = 0·1 mm; i to scale 4 = 0·05 mm.

Second maxilliped: Setation of basis and of endopod unchanged; exopod with 6 terminal plumose setae, an incipient 7th present in some specimens.
Third maxilliped: Not developed.
Pereiopods: Not developed.
Abdomen (Fig. 2b, 3b): Dorsal surface of 1st segment with a small setule; posterio-lateral processes longer than those of first zoea.

THIRD ZOEA

Dimensions: T.T. 1·7–1·8 mm, C.L. 0·7–0·8 mm.
Carapace (Fig. 1c): Posterio-lateral margin with 3–5 setules; dorsal margin with elevation more pronounced and the angular submedian lobes of rostral base more developed than those of second zoea.
Antennule (Fig. 1g): Now with an extra seta.
Antenna (Fig. 1k): Spinous process and exopod unchanged; endopod bud prominent, reaching for nearly $\frac{1}{4}$ length of spinous process.
Mandible: Unchanged.
Maxillule (Fig. 4c): Setation of endopod unchanged; basal endite with 9 spines/setae; setation of coxal endite unchanged.
Maxilla (Fig. 5a,d): Setation of endopod unchanged; basal endite with 5+5 setae; coxal endite setation unchanged; scaphognathite with 19 plumose setae.
First maxilliped (Fig. 4h): Setation of basis unchanged; 5th segment of endopod almost as long as 4th and with 5+1 setae; exopod with 8 terminal plumose setae.
Second maxilliped: Setation of basis and of endopod unchanged; exopod with 8 (in some specimens 9) terminal plumose setae.
Third maxilliped: Now represented as a small bud.
Pereiopods: Present as unsegmented buds.
Abdomen (Figs 2c, 3c): with 6 segments + telson; posterio-lateral processes longer than those of second zoea; 1st segment with 2 median setules on dorsal surface;·segments 2–5 with incipient pleopod buds; innermost lateral spinule of telson forks very minute, posterior margin of telson with 8 setae.

FOURTH ZOEA

Dimensions: T.T. 2·3–2·4 mm, C.L. 0·9–1·0 mm.
Carapace (Fig. 1d): Dorsal spine with 2–3 small setules near base; angular submedian lobes of rostral base more developed than those of third zoea.
Antennule (Fig. 1h): With 9–10 aesthetascs and 1–2 setae.
Antenna (Fig. 1l): Endopod almost $\frac{1}{2}$ length of spinous process.
Mandible (Fig. 1m): Mandibular palp represented as an unsegmented bud.
Maxillule (Fig. 4d): Setation on endopod unchanged; basal endite with 11 spines/setae; coxal endite with 9 setae.
Maxilla (Fig. 5b,e): Endopod setation unchanged; basal endite with 6+5 setae; coxal endite with 4+7 setae; scaphognathite with 27–28 plumose setae.
First maxilliped: Setation of basis and of endopod unchanged; exopod with 10 terminal plumose setae.
Second maxilliped: Setation of basis and of endopod unchanged; exopod with 10 (11 in some specimens) terminal plumose setae.
Third maxilliped: Represented as a larger bud than in the third zoea.
Pereiopods: First sub-chelate, 2nd–5th incipiently segmented.
Abdomen (Figs 2d, 3d): Segments 2–5 with well developed pleopod buds, 6th with posterio-lateral margins obtusely produced; dorsal surface of 1st segment with 4 setules; dorsal surface of telson with 2 setules, posterior margin with 9 setae.

MEGALOPA

Dimensions: C.L. 1·40 mm.
Carapace (Fig. 6a–c): Posteriorly slightly broadened, without tubercles, urogastric region elevated, a pair of indistinct carinae on orbital, protogastric, epibranchial and mesobranchial regions; hepatic regions slightly inflated; frontal region broad, with a narrow, truncate, medially concave rostrum directed obliquely downwards, submedian lobes rounded; dorsal surface and margins of carapace setose.
Eyes: Prominent, cornea slightly broader than peduncle.
Antennule (Fig. 7f): Peduncle 3-segmented, sparsely setose; exopod 4 segmented with a total of 14–15

aesthetascs, 4th segment long, thin and with one terminal and one subterminal seta, 1–2 small setae on segment 3; endopod 2-segmented, distal segment long, with 4 distal setae.

Antenna (Fig. 7g): Peduncle 3-segmented, with 2,2,2 setae respectively; flagellum 8-segmented, with 0,0,2,0,4,0,4,3 setae respectively.

Mandible (Fig. 7i): mandibular palp 2-segmented, distal segment short and broad, with 10–11 setae.

Maxillule (Fig. 7a–c): Endopod reduced and unsegmented, with 3 proximal and 2 terminal setae; inner margin of basal endite with 3 setae, distal margin with a total of 17 spines/setae; coxal endite with 14–15 setae.

Maxilla (Fig. 7d,e): Endopod reduced to subcylindrical, terminally acute lobe with 1–2 long setae; basal endite with 9 + 6 setae; coxal endite with 6 + 9 setae; scaphognathite with 49–50 short plumose setae.

First maxilliped (Fig. 6d): Inner margin of coxal endite with 10–11 setae and with 1–2 proximal setae; inner margin and outer surface of basis with 21–22 setae; endopod with 4–5 short setae; exopod 2-segmented, proximal segment with 2 distal setae, distal segment with 5 long terminal setae; epipod well developed, with 1–2 setae.

Second maxilliped (Fig. 6e): Proximally almost devoid of setae; merus of endopod with 2 setae, carpus with 1–2, propodus with 4 setae and one spine, dactylus with 7 stout thin spines and 2 setae; exopod long, distal segment with 5 long terminal setae; 2 epipods bearing distal setae and one additional endite present.

Third maxilliped (Fig. 6f): Coxa and basis not differentiated, with 3–5 setae; margins and outer surface of endopod ischium with 18–22 setae distributed as shown, merus with 5–6 setae on inner upper surface, carpus with 4–5 setae, propodus with 5–6, dactylus with 7–8 setae; exopod 2-segmented, distal segment with 5 long and one shorter terminal setae; epipod long, with 6–7 setae.

Cheliped (Fig. 6g): Stout, moderately setose, ischium with a prominent curved spine; inner margin of propodal prolongation and of dactylus cut into obtuse and sub-acute teeth.

Pereiopods 2–5 (Fig. 6h–k): Thin and setose, without ischial or basal spines; inner margin of dactylus of pereiopods 2–4 with 3,3,2 spines respectively; dactylus of 5th pereiopod with 3 long sub-distal setae, one small spine and a minute spinule.

Abdomen & telson (Fig. 7h–k): With 6-segments + telson and with numerous setae distributed as shown; posterio-lateral margins of segments suboval; segment 6 short. Telson truncate, broader than long, posterior margin slightly concave, with 3 long plumose setae, 2 pairs of dorsal and one pair of ventral setae on telson surfaces. Exopods of 1st–4th pleopods with 15–16, 15, 16, 13–14 long plumose setae; exopods decreasing in length progressively from 1st–4th, that of 4th only slightly longer than peduncle; endopods with 2 or 3 coupling hooks on internal margin. Uropod without endopod, with 10 marginal setae on exopod distal segment, proximal segment with one seta.

Remarks

A comparison of the present reared material of *Panopeus occidentalis* with the larval account of *P. herbstii* by Costlow & Bookhout (1961*b*) has revealed few differences between the zoeal stages of these two species but significant ones between the megalopas. These differences are summarised in Table 2. Details of setal patterns on the zoeal carapace, the first abdominal segment and telson, and on the abdominal segments of the megalopa of *P. herbstii* are not known. The submedian lobes of the carapace of *P. occidentalis* fourth zoea are not developed into the acute protrusions figured for this corresponding stage of *P. herbstii*. The megalopa of *P. occidentalis* is without the prominent 'rostral horns' figured for *P. herbstii* and in this respect it resembles the megalopa of *P. turgidus* (see Martin *et al.*, 1984, fig. 8(a)), a species placed by Abele (1970) into the genus *Eurypanopeus*. However, *P. turgidus* has long serrate spines on the posterior margin of the telson whereas *P. occidentalis* has relatively short plumose setae. It would appear that at least two types of megalopas are represented among closely related species assigned to the problematical genus *Panopeus* (viz. *P. herbstii, P. occidentalis* and *P. turgidus*). However, the zoeae of all three species can be clearly attributed to group I of the xanthid groups proposed by Martin (1984).

Larval stages are known for only 14 (see Table 1) of the 31 or more species of xanthid crabs reported from Bermuda waters (see Markham & McDermott, 1981). Published accounts of four of these, *Heteractaea ceratopus* (Stimpson), *Xantho denticulatus* (White), *Leptodius parvulus* Rathbun and *Eurytium limosum* (Say) are inadequate even for superficial comparative studies. The first zoea attributed to *Panopeus bermudensis* (Benedict & Rathbun) by Lebour (1944: 119,

Table 1 Published accounts of larval and juvenile xanthoidean crabs reported from Bermudan waters.

Carpilius corallinus (Herbst)	Laughlin *et al.* 1983: 171–12, figs 1–11 (1st–5th zoeae).
Eurypanopeus depressus (Smith)	Birge 1883: 414, Pl. XXXI, fig. 12, Pl. XXXII, fig. 13 (2nd zoea); Hyman, 1925: 8–9, Pl. 1, figs 2,4,8,14,18, Pl. 2, figs 24,28,32, Pl. 9 (1st zoea); Costlow & Bookhout 1961*a*: 7–13, figs 1–41 (1st–4th zoeae, megal.); Martin *et al.* 1984: 562, 565, 574, 588, figs 10*d*,*11d*, *13d*iv,16,20, 23*d*iv,28,29,33*d*iv,40,41,42,46 (1st, 2nd, 3rd, 5th crab).
Eurytium limosum (Say)	Kurata *et al.* 1981: 19–25, figs 1–4 (1st–4th zoeae, megal. 1st crab); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
Heteractaea ceratopus (Stimpson)	Gurney 1936: 628, Pl. VII, figs 69–71 (1st zoea).
Lobopilumnus agassizii (Stimpson)	Lebour 1950: 377, fig. 7 D,E (1st zoea, as var. *bermudensis*).
Micropanope sculptipes Stimpson	Andryszak & Gore 1981: 490–502, figs 1–6 (1st–4th zoeae, megal.).
Panopeus bermudensis Benedict & Rathbun	?Lebour 1944: 119, fig. 9 (1st zoea); Martin *et al.* 1984: 545–50, 556–7, 563–4, 566–9, 557–9, figs 2–5, 10a, 11a, 12, 13*a*i, 17, 21, 22, 23*a*i, 30, 31, 32, 33*a*i, 46, 47 (4th zoea, megal. 1st 2nd, 3rd, 5th crab).*
Panopeus herbstii H. Milne Edwards	Hyman, 1925: 9, Pl. 1, figs 5, 9, 15, 19, Pl. 2, figs 21, 25, 29, 33, Pl. 10, figs 116–124 (prezoea, 1st zoea); Costlow & Bookhout 1961*b*: 33–39, figs 1–6 (1st–4th zoeae, megal.); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated); Martin *et al.* 1984: 557–9, 564, 569, 579, figs 10b, 11b, 13*b*ii, 14, 18, 23*b*ii, 24, 25, 33*b*ii, 34, 35, 36, 46, 47 (1st, 2nd, 3rd, 5th crab).
Panopeus occidentalis de Saussure	present account.
Pilumnus dasypodus Kingsley	Sandifer 1974: 379–88, figs 1–6 (1st–4th zoeae, megal.); Bookhout & Costlow 1979: 2–13, figs 1–7 (1st–4th zoeae, megal); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
Pilumnus sayi Rathbun	McDonald & Lang 1976: 219 (abstract, no descript.); Bookhout & Costlow 1979: 13, fig. 7B (comp. with *P. dasypodus*, megal. abd. pereiopods figs); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
Pseudomedaeus agassizii (A. Milne Edwards)	Costlow & Bookhout 1968: 205–211, figs 1–5 (1st–4th zoeae, megal. as *Leptodius agassizii*); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
Xantho denticulatus (White)	Lebour 1944: 119, fig. 8 (1st zoea, as *Xanthodius denticulatus*).
Xanthodius americana (de Saussure)	?Lebour 1944: 119, fig. 7 (1st zoea, as *Leptodius parvulus*).

fig. 9) is almost certainly not this species (see Martin *et al.*, 1984: 541) and is assigned by Martin (1984) to his group II. Also questionable is the identification of the first stage zoea attributed by Lebour (1944: 119) to *Leptodius parvulus* (Fabricius) (see Wear, 1970: 86) and placed by Martin (1984) into group II; both of these above mentioned zoeae are 'piluminid types' (see Rice, 1980: 327). Lebour (1944) reported *'Leptodius parvulus'* as 'common in rocks and under stones between tide marks' but Verrill (1908: 340) noted it as 'a rare species at the Bermudas'. Markham & McDermott (1981: 1273) refer to this species as *Xanthodius americana* (de Saussure).

Martin (1984) has provided a useful key to the known xanthid zoeae of the American western Atlantic that will enable their identification to the groups he proposed and, in some instances, to species. In a more restricted context the combined features listed below may be adequate for distinguishing the zoeae of *Panopeus herbstii* and *P. occidentalis* from those of other species reported from Bermuda waters (see Table 1), except for *H. ceratopus* (that is insufficiently described) and

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*Martin, J. W., *et al.* 1985. Journal of Crustacean Biology 5 (I): 84–105 (1st–4th zoeae, megal.).

Table 2

	P. herbstii	*P. occidentalis*
FIRST ZOEA		
Antennule		
aesthetascs:	3	3
setae	2	1
Antenna		
spinous process	distal $\frac{1}{4}$ spinulate	distal $\frac{1}{2}$ spinulate
proximal spinule on spinous process	?absent	present
terminal seta on exopod	1	2
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
Maxilla		
scaphognathite	4 plumose setae + apical projection	3 plumose setae + apical projection
Carapace		
dorso-median elevation	?not prominent	prominent
SECOND ZOEA		
Antennule		
aesthetascs	3	4
setae	2	1
Antenna		
spinous process	distal $\frac{1}{3}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
THIRD ZOEA		
Antennule		
endopod bud	developed	not developed
aesthetascs	3	4
Antenna		
spinous process	distal $\frac{1}{6}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
Maxilla		
scaphognathite	18 plumose setae	19 plumose setae
FOURTH ZOEA		
Antennule		
exopod	segmented	not segmented
Antenna		
spinous process	distal $\frac{1}{6}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
basal endite	12 spines/setae	11 spines/setae
Maxilla		
basal endite	13 setae	11 setae
coxal endite	9 setae	11 setae
scaphognathite	25 plumose setae	27–28 plumose setae
MEGALOPA		
Carapace	almost as broad as long	much longer than broad
submedian lobes of frontal region	produced into spines	obtuse
Antennule		
aesthetascs on exopod	18	14–15
exopod 4th segmt. subterminal setae	2	1

continued overleaf

Table 2—*continued*

	P. herbstii	*P. occidentalis*
endopod segments	1	2
disto-external margin 3rd ped. segment	with long setae	without setae
Antenna		
flagella segments	7	8
setation, ped. segments 1–3	2,1,1	2,2,2
Maxillule		
setation of endopod	7	5
basal endite	approx. 22 spines/setae	20 spines/setae
Maxilla		
endopod	not noticeably reduced, with many setae	reduced, with 1–2 setae
basal endite	18 setae (10+8)	15 setae (9+6)
coxal endite	14 setae	15 setae
First maxilliped		
setation of basis	18	21–22
endopod	terminally acute	spatulate
exopod	segments almost subequal	proximal segment longest
exopod distal segment	6 terminal setae	5 terminal setae
proximal segment	1 outer distal seta	2 outer distal setae
Second maxilliped		
endopod, propodus	?without a disto-external spine & with 6 setae	with a disto-external spine & with 4 setae
dactylus	13 spines/setae	7 spines & 2 setae
Third maxilliped		
inner margin of ischium	10 setae	13–14 setae
Pleopods		
setation of exopods 1–4	15,15,15,12	15–16,15,16,13–14
setation of uropod exopod	8	10
Telson		
posterior margin	with 2 long setae/spines and 3 short setae	with 3 short plumose setae

the first zoea of *E. limosum* (from which it cannot be separated at present). 1. Carapace lateral spines present (absent in *P. bermudensis* Benedict & Rathbun). 2. Dorso-lateral processes present only on 2nd and 3rd segments of abdomen (on 2nd–5th segments in '*P. bermudensis* Lebour'). 3. Antennal exopod small (as long as spinous process in *P. sayi, P. dasypodus, X. americana* and *L. agassizii*; half as long in *C. corallinus*). 4. Posterio-lateral processes of abdomen short in first zoea and submedian lobes of rostral base not developed as 'pre-orbital spines' from second zoea onwards (posterio-lateral processes long in first zoea and a pair of long 'pre-orbital' spines present from second zoea onwards in *P. agassizii*). 5. Each telson fork with 2 lateral spines, one sometimes minute (only one lateral spine present in all stages of *M. sculptipes* and *E. depressus* and from second stage onwards in *E. limosum*). 6. Spinous process of antenna spinulate (?smooth in *X. denticulatus*). The megalopa of *P. occidentalis* is without 'rostral horns' (i.e. protrusions of the submedian lobes), a feature which readily distinguishes it from the megalopas of other Bermuda xanthids known at present except for *P. dasypodus* and *P. sayi* from which it is separated by having only a prominent curved ischial spine on the first pair of pereiopods and no ischial or coxal spines on the second to fifth pairs.

Acknowledgements

The visit to the Bermuda Biological Station was partly sponsored by an Exxon Corporation Fellowship. I wish to thank Dr Wolfgang Sterrer, Director of the Biological Station and his staff for providing the facilities for holding ovigerous crabs and for their assistance with various matters during my visit. Dr A. L. Rice kindly read the manuscript.

References

Abele, L. G. 1970. *The marine decapod Crustacea of the northeastern Gulf of Mexico*. Masters Thesis, Florida State University. Tallahassee, Florida (not seen).

Andryszak, B. L. & Gore, R. H. 1981. The complete larval development in the laboratory of *Micropanope sculptipes* (Crustacea, Decapoda, Xanthidae) with a comparison of larval characters in western Atlantic xanthid genera. *Fishery Bulletin of the U.S. Fish and Wildlife Service*. Washington D.C. **79:** 487–506.

Birge, E. A. 1883. Notes on the development of *Panopaeus sayi* (Smith). *Studies from the Biological Laboratory, Johns Hopkins University*. Baltimore. **2** (4): 411–426.

Bookhout, C. G. & Costlow, J. D. 1979. Larval development of *Pilumnus dasypodus* and *Pilumnus sayi* reared in the laboratory (Decapoda Brachyura, Xanthidae). *Crustaceana. International Journal of Crustacean Research*. Leiden. Supplement **5:** 1–16.

Costlow, J. D. & Bookhout, C. G. 1961*a*. The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. *Crustaceana. International Journal of Crustacean Research*. Leiden. **2:** 6–15.

—— 1961*b*. The larval stages of *Panopeus herbstii* Milne-Edwards reared in the laboratory. *Journal of the Elisha Mitchell Scientific Society*. Chapel Hill, N.C. **77:** 33–42.

—— 1968. Larval development of the crab, *Leptodius agassizii* A. Milne Edwards in the laboratory (Brachyura, Xanthidae). *Crustaceana. International Journal of Crustacean Research*. Leiden. Supplement **2:** 203–213.

Gurney, R. 1936 Notes on some Decapod Crustacea of Bermuda—III–V. *Proceedings of the Zoological Society of London* **3:** 619–630.

Hyman, O. W. 1925. Studies on the larvae of crabs of the family Xanthidae. Proceedings of the United States National Museum. Washington, D.C. **67:** 1–22.

Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia: Part III. Larvae of decapod Crustacea of Georgia. *Unpublished report. University of Georgia Marine Institute*. Sapelo Island (not seen).

——, Heard, R. W. & Martin, J. W. 1981. Larval development under laboratory conditions of the xanthid mud crab *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) from Gerogia. *Gulf Research Reports*. Gulf Coast Research Laboratory, Ocean Springs, Mississippi **7:** 19–25.

Laughlin, R. A., Rodriguez, P. J. & Marval, J. A. 1983. Zoeal stages of the coral crab *Carpilius corallinus* (Herbst) (Decapoda, Xanthidae) reared in the laboratory. *Crustaceana. International Journal of Crustacean Research* **44:** 169–186.

Lebour, M. V. 1944. II. Larval crabs from Bermuda. *Zoologica*, New York **29:** 113–128.

—— 1950. Notes on some larval decapods (Crustacea) from Bermuda. *Proceedings of the Zoological Society of London* **120:** 369–379.

Markham, J. C. & McDermott, J. J. 1981. A tabulation of the Crustacea Decapoda of Bermuda. *Proceedings of the Biological Society of Washington* **93:** 1266–1276.

Martin, J. W. 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the Western Atlantic and Gulf of Mexico. *Bulletin of Marine Science*, Coral Gables **34:** 220–239.

——, Felder, D. L. & Truesdale, F. M. 1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura). *Philosophical Transactions of the Royal Society of London* B **303:** 537–604.

McDonald, H. J. & Lang, W. 1976. The larval development of *Pilumnus sayi* Rathbun reared in the laboratory. *American Zoologist*. Utica, N.Y. **16:** 219.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. *Bulletin of the United States National Museum*. Washington D.C. **1523:** i–xvi, 1–610.

Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* **35:** 271–424.

—— & Ingle, R. W. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bulletin of the British Museum (Natural History) Zoological Series*. London **28:** 101–119.

Sandifer, P. A. 1974. Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory. *Bulletin of Marine Science*. Coral Gables. **24:** 378–391.

Saussure, H. de 1857. Diagnosis de quelques Crustacés nouveaux de l'Amerique tropicale. *Revue et Magasin de Zoologie Pure et Appliquée*. Paris **9:** 501–505.

Verrill, A. E. 1908. Decapod Crustacea of Bermuda; 1–Brachyura and Anomura. Their distribution, variations, and habits. *Transactions of the Connecticut Academy of Arts and Sciences*. New Haven **13:** 299–474.

Wear, R. G. 1970. Notes and bibliography on the larvae of xanthid crabs. *Pacific Science*, Honolulu **24:** 84–89.

Williams, A. B. 1965. Marine Decapod Crustaceans of the Carolinas. *Fishery Bulletin of the U.S. Fish and Wildlife Service*. Washington, D.C. **65:** i–xi, 1–298.

Manuscript accepted for publication 12 December 1984

Addendum

Recently, Williams, A. B. 1983. Fishery Bulletin of the National Oceanic and Atmospheric Administration. Washington, D. C. 81 4: 868–872 (published October 1984) assigned bermudan material of *P. herbstii* to *P. lacustris* Desbonne, 1867

A revision of the spider genera *Holcolaetis* and *Sonoita* (Araneae: Salticidae)

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Introduction

This present paper revises two closely related genera, *Holcolaetis* Simon, comprised of five species and *Sonoita* Peckham and Peckham, which is monotypic. Their geographical distribution is African, with the exception of one species of *Holcolaetis* which also occurs in North Yemen. Species of *Holcolaetis* are usually large, flattened and hairy, they are well camouflaged in life and superficially resemble species of *Marpissa* C. L. Koch, a large genus with several well known European species. They seem to be well adapted for living in confined spaces and much of their time is probably spent on tree trunks, however, they have also been found on cacti in association with the webs of other spiders. The only known species of *Sonoita* is on the other hand small and not flattened. The biology is unknown. Both groups, unlike many salticid genera, can be easily recognised not only by their general habitus, but by the presence of large posterior median eyes and also rather distinctive genitalia.

The taxonomy of *Holcolaetis* has been unusually muddled, primarily because Simon (1907) appears to have misidentified the type species subsequent to his original description. Further difficulties have arisen, in *Holcolaetis* especially, from a shortage of specimens making it difficult to match males and females, details of which are referred to in the descriptions. Compounding these problems is the fact that the epigynes of *Holcolaetis* females are unusually variable and also often plugged, both in the region of the copulatory openings and on the posterior margins.

The presence of large posterior median eyes in species of both genera, palpal median apophyses and abdominal pustuliform organs suggests that they belong in one of the more primitive branches of the Salticidae.

The standard abbreviations and measurements are those used by Wanless (1978), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Genus *HOLCOLAETIS* Simon

Holcolaetis Simon, 1886: 394. Type species *Holcolaetis xerampelina* Simon, by monotypy. Simon, 1901: 452–454. Waterhouse, 1902: 414. Petrunkevitch, 1928: 181. Dyal, 1935: 218, 222. Neave, 1939: II: 671. Roewer, 1954: 937; 1965: 22. Bonnet, 1957: 2222. Prószyński, 1971: 417. Wanless, 1984: 136.
Holcolethis Simon 1909: 413. Neave, 1939: II: 671. [lapsus calami].

Definition. Flattened hairy spiders; medium to large in size i.e. total length between 4·0 and 16·0 mm; sexes alike except males usually have longer more slender legs; colour patterns interspecifically similar—the abdomen characteristically marked with a broad dorsal dentate band; anterior leg spines strong on femora, otherwise absent or few and minute; males, females and subadults with pustuliform field more or less anterior to the first pair of abdominal apodemes.

Carapace: low, longer than broad, widest at about level of coxae II–III with transverse depression between posterior lateral eyes and fovea; fovea moderately long, positioned well behind posterior lateral eyes. *Eyes:* with moderately pronounced lenses set on low tubercles; laterals with black surrounds; anteriors closely set, equally or subequally spaced with apices procurved in frontal view; anterior laterals equal to or greater than half diameter of anterior medians; posterior medians relatively large, closer to and just outside optical axis of anterior laterals; posterior laterals more or less as large as anterior laterals and positioned well inside

Issued 31 October 1985

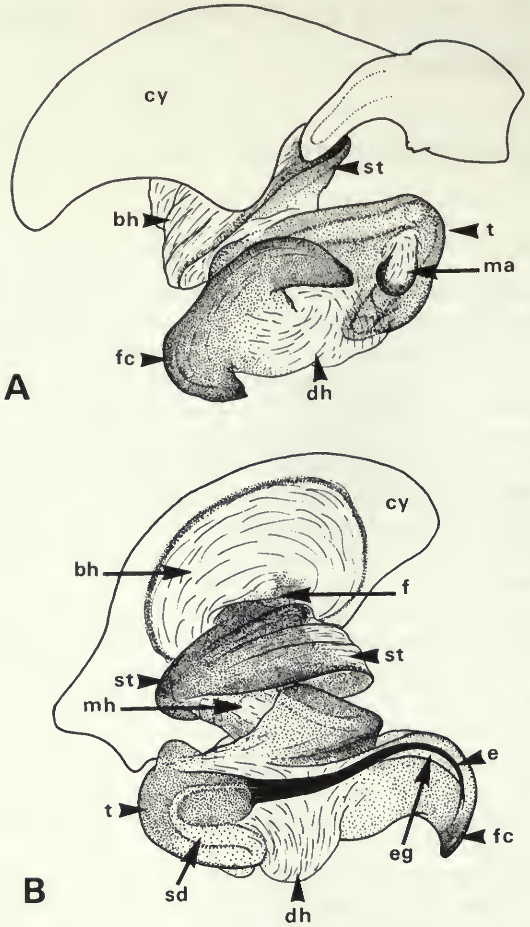

Fig. 1 *Holcolaetis vellerea* Simon, ♂, expanded palp: A, retrolateral view; B, prolateral view. Abbreviations: bh, basal haematodocha; cy, cymbium; dh, distal haematodocha; e, embolus; eg, embolic guide; f, fulcrum; fc, functional conductor; ma, median apophysis; mh, median haematodocha; sd, seminal duct; st, subtegulum; t, tegulum.

lateral margins of carapace when viewed from above; posterior ocular quadrangle broader than long and slightly wider behind; entire quadrangle occupying between 35 and 43% of carapace length. *Clypeus:* low, between 10–26% of diameter of anterior median eyes. *Chelicerae:* robust, usually more bulbous in female; inclined anteriorly, more or less parallel; promargin with 4–6 teeth, retromargin with 6–10. *Maxillae:* long and diverging. *Labium:* longer than broad, about half maxillar length. *Sternum:* elongate scutiform, more attenuate in females. *Pedicel:* short. *Abdomen*: elongate ovoid with dorsal dentate band and indistinct pustuliform field; spinnerets moderately long, anteriors and posteriors more or less equal in length, but unequally robust, medians shorter and more slender, spigots of anterior spinnerets compact except for a single pair of longer spigots on inner margin, present in both sexes, but evidently more pronounced in females; former position of colulus indicated by group of setae between tracheal slit and base of anterior spinnerets; tracheal system apparently simple (only examined in *H. vellerea* Simon), the opening an obscure slit, not usually evident, just in front of the anterior spinnerets. *Legs:* moderately long and robust, strongest in females; anteriors often with strong fringes; claws smooth or pectinate; scopulae absent; tufts present; spines moderately strong, most numerous on posterior legs, on legs I usually lacking except on femora, basic pattern rather variable. *Female palps:* moderately long with an apical claw, distal segments sometimes darker than proximal ones.

Epigynes: Intergenerically and interspecifically fairly distinct, but intraspecifically sometimes variable and often plugged, both in area of copulatory openings and posterior margin. Generally characterised by delicate translucent posterior median flanges variable in development and occasionally damaged. Copulatory openings indistinct usually because of heavily sclerotised surrounds (Fig. 16); introductory ducts broad, moderately long, sometimes looped with separate or evidently fused glandular appendices (arrowed, Figs 4I; 16B,C) spermathecae rounded to avoid, relatively large and dark; fertilisation ducts leaf-like, obscured by dorsal membrane and apparently supported by apodemes.

Male palps: Intergenerically and interspecifically fairly distinct; complex and often rather dark; tibiae short to moderately long with robust prong-like retrolateral apophyses, some bearing pronounced flanges; cymbium with pronounced retrolateral lobe (arrowed, Fig. 3C), a small prolateral basal protuberance (arrowed, Fig. 3A) and distal scopula; embolus moderately long robust and curving sometimes partly hidden by embolic guide of functional conductor; distal haematodocha evident, in the unexpanded palp, as an oblong membraneous fold (arrowed, Fig. 3A) contiguous with the tegulum and functional conductor; tegulum broadly crescent-shaped (anterior portion obscured by functional conductor) containing a wide sinuous seminal duct and bearing occasionally a pronounced prolateral flange (arrowed, Fig. 8B–D); functional conductor large with an embolic guide and sometimes a massive prong; median apophysis bowl-like, but shallow and arising from membraneous region of the tegulum, in reality contiguous with the distal haematodocha; median haematodocha short and tube-like; subtegulum a ribbed ring-like sclerite, form of seminal reservoir indistinct; basal haematodocha large and bladder-like, i.e. in expanded palp.

REMARKS. There is no evidence as yet to support the hypothesis that pustuliform fields are pheromone dispersal sites. Furthermore, spheres found scattered over the organs and lodged in their pores (Wanless, 1984*b*) are probably contaminants (Humphreys, 1985) as they are consistent with the spheres covering the chorion of spiders eggs (Humphreys, 1983). The occurrence of *H. vellerea* in close proximity to alien egg-sacs (see below) and their egg guarding behaviour (Fig. 19) would undoubtedly expose them to such contamination.

The internal epigynal structures are usually very dark (Fig. 16) and deeply embedded in connective tissue which obscures detail even in lactic acid preparations. Although easily removed with fine entomological pins the process results in the destruction of the dorsal membrane, referred to above, which is consequently not shown in some of the vulvae illustrations, for example compare Figs 7D and 7E.

Hinge lines (Parry, 1957) are a common, but possibly overlooked feature of spider legs, they are in effect modifications of the cuticle indicating the site of muscle attachment. In *Holcolaetis* they are fairly conspicuous and usually evident, at low magnifications, as a pair of longitudinal bands on the dorsal surface of the tibiae, patellae and distal portion of the femora; on the last two segments they sometimes form patches rather than lines.

When examined by SEM, hinge lines are seen to be comprised of a series of triangular plates (Fig. 15) suggesting that they may provide for a degree of flexibility within the cuticle. The development and extent of hinge lines in other Salticidae is uncertain, casual observations with the optical microscope shows that they are not always evident and in general they are more conspicuous in dark robust legs than in pale slender ones. In other spider families, for example, the Thomisidae, they are sometimes well developed and clearly influence leg colour patterns, especially longitudinal markings. Similar cuticular structures have been noted in mites (Prof. G. O. Evans, pers. comm.) who also suggests that in areas where the cuticle is thin they may have a ventilatory function and allow for gaseous exchange at the site of muscle insertion.

DIAGNOSIS. *Holcolaetis* known only from Africa and N. Yemen may be distinguished from all other salticid genera by the large posterior median eyes and flattened body form.

AFFINITIES. *Holcolaetis* is undoubtedly close to *Sonoita*, the relationship being supported by four possible synapomorphies, namely the characteristic form of the tegulum, median apophysis and distal haematodocha in males and epigynal flanges in females. Furthermore, pustuliform fields are present in both genera, but in *Sonoita* they are obscured by setae and comprised of fewer, more scattered pustuliform organs (Figs 13, 14).

Wanless (1982, 1984*a*, 1984*b*) suggested that on the basis of certain palpal characters (i.e. the presence of a movable median apophysis and pronounced functional conductor, (reduced in *Allococalodes* Wanless) that *Holcolaetis* and *Sonoita* were allied to *Cocalodes* Pocock and *Allococalodes* and furthermore they formed a group, the *Cocalodes*-group, which probably merited subfamilial rank. The hypothesis although seemingly tenable is open to question since it cannot be supported by other characters and furthermore, both the median apophysis and functional

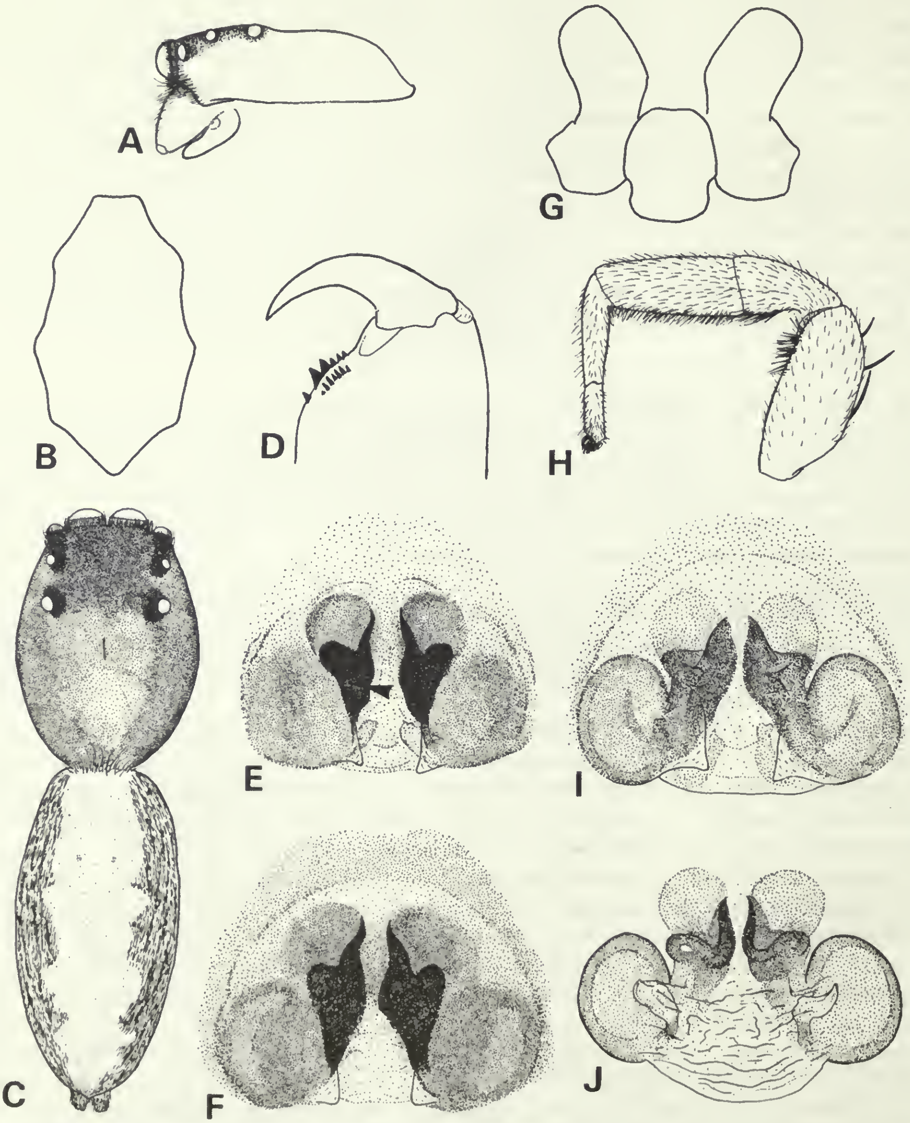

Fig. 2 *Holcolaetis xerampelina* Simon, lectotype ♀: B, sternum; C, dorsal; D, chelicera; F, epigyne. ♀ from Zambia: A, carapace, lateral view; E, epigyne; G, maxillae and labium; H, leg I; I, vulva, outer view; J, vulva, inner view.

conductor may have arisen several times within the Salticidae. An alternative grouping based on the assumption that the abdominal 'secretory' organs (see Wanless, 1984*b*) i.e. mytiliform and pustuliform fields, together with their specialized setae are homologous and synapomorphic for Spartaeinae and *Holcolaetis*/*Sonoita* is more acceptable. Unfortunately the incidence of abdominal 'secretory' fields in other spiders is largely unknown (see Wanless, 1984*b*) and since their presence can only be confirmed by SEM, they were initially overlooked in *Sonoita*, it is clear that earlier, possibly erroneous assumptions regarding their absence in *Cocalodes* and *Allococalodes* will have to be reviewed.

BIOLOGY. Little is known of the biology of *Holcolaetis,* collectors notes suggest that most species probably live on tree trunks. R. R. Jackson (pers. comm.) found *Holcolaetis vellerea* Simon, in Kenya, on the trunks of *Euphorbia* and cacti. There were no nests and some females were seen sitting on egg-sacs (Fig. 19A, B). The plants were wrapped up in webs, especially araneid webs and the *Holcolaetis* were sitting with araneid silk over them, usually very close. Sometimes they were under the edges of the silk of araneid egg-sacs, but they were never seen actually standing on alien silk.

Check list and distribution of species in the genus *Holcolaetis*

Holcolaetis (* = type species)

H. albobarbata Simon	Angola; Cameroon; Uganda.
H. clarki sp. n.	Angola; Cameroon; Ghana; Zaire.
H. vellerea Simon	Angola; Cameroon; Ivory Coast; Kenya; N. Yemen; Rwanda; São Thomé; Zaire.
**H. xerampelina* Simon	Malawi; Tanzania; Zambia.
H. zuluensis Lawrence	South Africa; Tanzania.

Key to species of *Holcolaetis*

Males

1 Functional conductor with massive apophysis (arrowed, Figs 3A; 5A; 6A); tegular flange absent 2
– Functional conductor without an apophysis; tegular flange present (arrowed, Figs 8B; 10A) . 4
2 Tip of functional conductor sinuous; retrolateral tibial apophysis with pronounced flange (arrowed, Fig. 6A) (Kenya; South Africa; Tanzania) . . ***zuluensis*** Lawrence (p. 259)
– Tip of functional conductor hardly if at all sinuous; retrolateral tibial apophysis without well developed flange 3
3 Embolus relatively robust and not obscured; distal haematodocha narrow (arrowed, Fig. 3A) (Malawi; Tanzania; Zambia) . . . . ***xerampelina*** Simon (p. 254)
– Embolus relatively slender and partly obscured; distal haematodocha broad (arrowed, Fig. 5A) (East, Central and West Africa; N. Yemen) . . . . . ***vellerea*** Simon (p. 255)
4 Retrolateral tibial apophysis with pronounced flange (arrowed, Fig. 10A, D) (Angola; Cameroon; Ghana; Zaire) . . . . ***clarki*** sp. n. (p. 263)
– Retrolateral tibial apophysis lacking pronounced flanges (Fig. 8A, B) (Angola; Cameroon; Uganda) . . . . ***albobarbata*** Simon (p. 262)

Females

1 Epigyne with conspicuous black copulatory openings more or less heart-shaped in profile (Fig. 2E) (Malawi; Tanzania; Zambia) . . . . ***xerampelina*** Simon (p. 254)
– Epigyne otherwise 2
2 Copulatory openings arising within a dark more or less ovate depression (Fig. 7A; B) (Angola; Cameroon; Uganda) . . . . ***albobarbata*** Simon (p. 260)
– Epigyne otherwise 3
3 Copulatory openings arising within rounded depressions (Figs 6E–G; 9C,D) 4
— Copulatory openings arising within a broad ill-defined depression—more evident in specimens than in Fig. 4D–F (East, Central and West Africa; N. Yemen) . ***vellerea*** Simon (p. 255)
4 Introductory ducts hardly if at all evident through uncleared integument (Fig. 9C, D) (Angola; Cameroon; Ghana; Zaire) . . . . ***clarki*** sp. n. (p. 263)
– Introductory ducts usually evident, especially black proximal regions (arrowed, Fig. 6G) Kenya; South Africa; Tanzania) . . . . ***zuluensis*** Lawrence (p. 259)

Holcolaetis xerampelina Simon
(Figs 2, 3, 16A)

Holcolaetis xerampelina Simon, 1886: 394. LECTOTYPE ♀ (here designated) Zanzibar, (MNHN, Paris). Simon, 1901: 453, 454; 1909 (1910): 413. Strand, 1909: 181. Petrunkevitch, 1928: 181. Roewer, 1954: 937. Bonnet, 1957: 2223. Prószyński, 1971: 417. Cutler, 1976: 132.

REMARKS. To judge from museum specimens and the literature there appears to have been some confusion over the identity of this species, primarily because Simon consistently identified *H. zuluensis* Lawrence as *H. xerampelina* Simon. Lessert (1925*a*) also misidentified *H. xerampelina* since the specimens he used for his illustrations are without doubt *H. zuluensis*. His identification was based on an earlier description by Strand *'Les pattes-machoires correspondent bien a la description de Strand* (1909, p. 181)'. Strand's description is fairly detailed, but in the absence of figures and specimens the species cannot be identified with certainty.

Roewer (1965) merely perpetuated the problem by producing crude copies of Lessert's figures, a feature noted by Clark (1974). From correspondence and notebooks of the late Mr Clark (BMNH) it is clear that he had correctly identified the majority of *Holcolaetis* species. Unfortunately, he misidentified the type specimen of *H. xerampelina*, selecting instead a specimen of *H. zuluensis* from Gabon that Simon had incorrectly identified as *H. xerampelina*. He therefore quite naturally assumed that *H. zuluensis* was a junior synonym. He did not, however, make a definite proposal (see Clark, 1974) and the synonymy was never accepted.

DIAGNOSIS. Similar to *H. vellerea and H. zuluensis,* but separated by the narrow element of the distal haematodocha in males (arrowed, Fig. 3A), and the black somewhat heart-shaped profile of the introductory ducts in females (arrowed, Fig. 2E).

FEMALE LECTOTYPE, in fair condition. *Carapace* (Fig. 2C) dark reddish ringed black in eye region with broad pale orange band on thoracic part; clothed in grey/pale golden pubescent hairs with whitish ones on thoracic band; eye region rubbed, probably white haired; also, on margins and submargins indistinct narrow bands of short white hairs. *Eyes:* laterals with black surrounds; fringed by white hairs with dull pale amber ones around lower rims of anteriors. *Clypeus:* covered in pale greyish hairs. *Chelicerae:* dark red with scattered long amber hairs; promargin with six

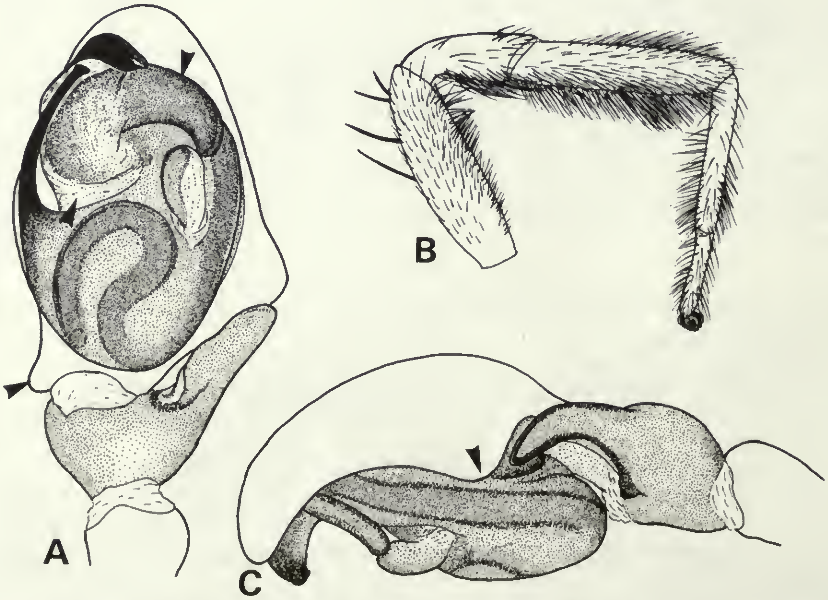

Fig. 3 *Holcolaetis xerampelina* Simon, ♂, A, palp, ventral view; B, leg I; C, palp, retrolateral view.

teeth, retromargin with seven. *Maxillae:* reddish with inner distal margins whitish yellow. *Labium:* dark reddish tipped whitish yellow. *Sternum* (Fig. 2B): yellowish orange with darker margins; shiny; thinly clothed in fine pale amber hairs with stronger whitish and amber hairs on margins. *Abdomen:* dorsum amber mottled black, clothed in amber hairs with broad central pale yellow dentate band clothed in pale creamy and scattered pale amber hairs; pustuliform field obscure; venter dirty pale yellow mottled black with three central black bands converging towards spinnerets; spinnerets amber tinged black. *Legs:* legs I (Fig. 2H): amber to dark amber lightly tinged black on tibiae; fringed with amber hairs on underside of tibiae, patellae and distal retrolateral side of femora; other legs generally amber with vague sooty annuli, dark on legs IV; also, on all legs scattered semirecumbent fringes of fine white hairs. Spines of legs I: femora p 0–3–0, d 0–2–2. *Palps:* pale yellow becoming amber distally and on basal part of femora. *Epigyne* (Fig. 2F): clothed in fine hairs.

Dimensions (mm): total length 12·5; carapace length 5·36, breadth 4·0, height 1·88; abdomen length 7·12; eyes, anterior row 2·76, middle row 2·78, posterior row 2·92; quadrangle length 1·92 (35% of carapace length). *Ratios.* AM : AL : PM : PL :: 18 : 9·5 : 7·1 : 10·5; AL–PM–PL :: 13–17; AM : CL :: 18 : 4.

MALE from Malawi, in fair condition formerly undescribed. *Carapace:* dark orange brown tinged black especially on sides and in eye region; irregularly clothed in whitish and dull amber hairs (rubbed) with scattered brown-black ones on sides; also, on lower sides a narrow submarginal band of short white hairs. *Eyes:* laterals with black surrounds; fringed by pale amber hairs with conspicuous white ones on inner and outer parts of upper rims of anterior medians and on inner part of upper rims of anterior laterals. *Clypeus:* clothed in amber and long black hairs. *Chelicerae:* orange-brown lightly tinged black; thinly clothed in brown-black hairs; promargin with five teeth, retromargin with seven. *Maxillae and labium:* orange-brown lightly tinged black with inner distal margins of maxillae whitish. *Sternum:* orange-brown tinged black; shiny; clothed in scattered white and brown-black hairs. *Coxae:* yellow-brown, first pair lightly tinged black. *Abdomen:* with dorsal greyish white dentate band containing vague blackish markings and chevrons; sides blackish with scattered long amber hairs; venter grey tinged black, clothed in vague whitish hairs laterally and short amber ones medially—the latter forming a vague longitudinal band; spinnerets yellow-brown tinged black. *Legs:* first and to a lesser extent second pairs densely fringed in black hairs (Fig. 3B); generally yellow-brown tinged black except for light yellow-brown tarsi and metatarsi. Spination of legs I: femora p 0–2–1, d 0–3–2. Palp (Fig. 3A,C).

Dimensions (mm): total length 7·92; carapace length 3·44; breadth 2·44, height 1·24; abdomen length 4·6; eyes, anterior row 1·94, middle row 1·88, posterior row 1·92; quadrangle length 1·4 (40% of carapace length). *Ratios:* AM : AL : PM : PL :: 15 : 8·2 : 6 : 7; AL–PM–PL :: 9–11; AM : CL :: 15 : ca. 2·5.

VARIATION. Another female measures 11·0 mm total length, 4·88 mm carapace length.

DISTRIBUTION. Malawi; Tanzania; Zambia.

MATERIAL EXAMINED. **Malawi:** Chintheche, 1♂, I–II.1976, *R. Jocque,* MT. 147.920. (MRAC, Tervuren). **Tanzania:** Zanzibar, lectotype ♀, + juvenile, *Raffray,* (MNHN, Paris, 987). **Zambia:** Lake Mweru, Wantipa, from tree, 1♀, ix.1944, *P. D. L. Ghilbride,* S.34, (BMNH. 1946.12.31.107).

Holcolaetis vellerea Simon
(Figs 1, 4, 5, 12, 15, 16B, 17–18)

Holcolethis vellerea Simon, 1909 (1910): 78. LECTOTYPE ♀, (here designated) São Thomé, (MNHN, Paris) [examined]; [*Holcolethis* lapsus for *Holcolaetis*].

Holcolaetis vellerea: Roewer, 1954: 937; 1965: 26. Bonnet, 1957: 2222. Prószyński, 1971: 417. Clark, 1974: 16.

Holcolaetis vidua Lessert, 1927: 426. Holotype ♂, Zaire, (AMNH, New York) [examined]. Dyal, 1935: 222 [?misidentification]. Roewer, 1954, 937: 1965: 27. Bonnet, 1957: 2223. Prószyński, 1917: 417. Clark, 1974: 16 [= *vellerea*].

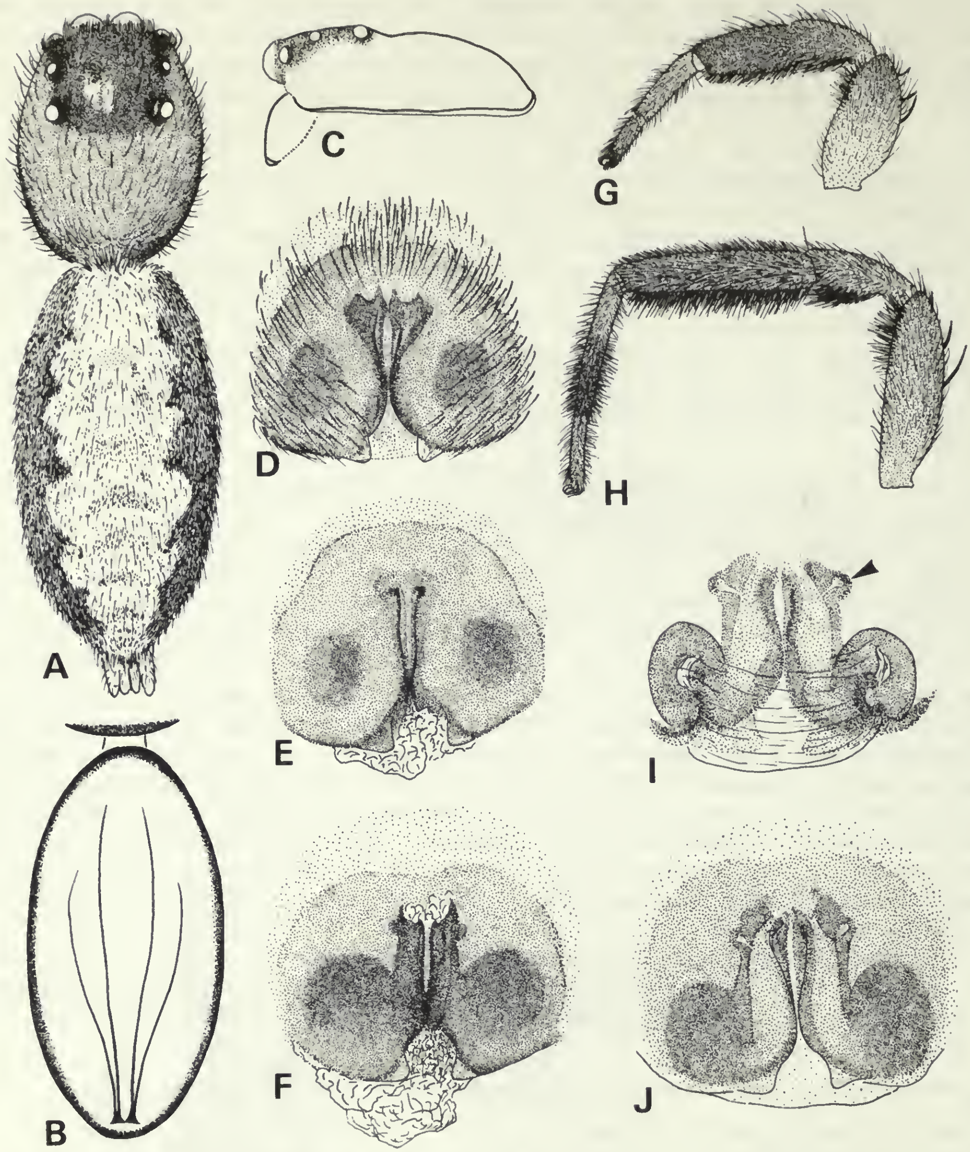

Fig. 4 *Holcolaetis vellerea* Simon, ♀ from Rwanda: A, dorsal view; B, tracheal system—schematic; C, carapace, lateral view; D, epigyne; F, epigyne, another specimen; G. leg I; I, vulva, inner view; J. vulva, outer view. ♀ from Kenya: E, epigyne. ♂ from Rwanda: H, leg I.

Holcolaetis camerunensis Roewer, 1965: 26. Holotype ♂ Cameroon, (FS, Frankfurt am Main) [examined]. Prószyński, 1971: 417. Brignoli, 1983: 640. **Syn. n.**

DIAGNOSIS. Similar to *H. zuluensis*, but separated by the relatively short tip of the functional conductor and absence of a pronounced flange on the retrolateral tibial apophysis in males (Fig. 5A). Females are distinguished, in spite of considerable epigynal variation and plugging, by the absence of rounded depressions surrounding the copulatory openings and also dark patches anterior to them. In reality the introductory ducts of *H. zuluensis* loop anteriorly and are visible through the integument as dark patches (arrowed, Fig. 6G). Whereas there are no such loops in *H. vellerea* and consequently no dark patches.

Male from Rwanda, in good condition. *Carapace:* reddish orange with blackish eye region, marginal and submarginal bands; thickly clothed in whitish and pale amber hairs with scattered bristles and pattern of marginal bands comprised of white hairs bordered above by a band of black hairs and below by dark bare cuticle edged in white hairs. *Eyes:* laterals with black surrounds; fringed by dull amber and white hairs with scattered bristles behind anterior row. *Clypeus:* clothed in dull amber hairs with marginal fringe of long black ones. *Chelicerae:* dark reddish; thinly clothed in black hairs; promargin with five teeth, retromargin with eight. *Maxillae and labium*: dark reddish, the former with yellow inner distal margins. *Sternum:* dark brownish orange lightly tinged black; thinly covered in black hairs—fine in centre, coarse on margins. *Coxae:* first pair dark reddish, others orange-brown. *Abdomen:* with dorsal greyish yellow dentate band clothed in fine whitish hairs and scattered bristles; sides mottled black with fine brown-black hairs and bristles; venter similar to sides, but with four inconspicuous greyish stripes containing lines of amber spots; spinnerets dark brown tinged black; clothed in black hairs with whitish ones on posterior pair. *Legs:* legs I dark brownish orange lightly tinged black with inside of femora, basal half of metatarsi and tarsi paler, densely fringed in brown-black hairs with long whitish ones on inside of femora and patellae; also semirecumbent tufts of white hairs on inside face of basal half of metatarsi; legs II similar, but paler markings in greater contrast; legs III dark orange-brown faintly tinged black with yellow-brown metatarsi and tarsi—the former with blackish apices, clothed in long whitish and grey-black hairs with scattered semirecumbent tufts of white ones; legs IV similar to III except metatarsi darker. Spination of legs I: metatarsi v 2–0–0; tibiae v 1–0–0; femora d 0–3–3, p 0–0–1. *Palp:* as in Fig. 5A–B, but darker.

Dimensions (mm): total length 10·2; carapace length 4·64, breadth 3·52, height 1·72; abdomen length 5·6; eyes, anterior row 2·38, middle row 2·32, posterior row 2·36; quadrangle length 1·8 (38% of carapace length). *Ratios:* AM : AL : PM : PL :: 18 : 9 : 6·6 : 9; AL–PM–PL :: 6·6–9; AM : CL :: 18 : ca. 4.

Female from Rwanda, in good condition. Similar to male. *Carapace* (Fig. 4A, C). *Eyes:* fringed by white hairs with some amber ones. *Clypeus:* clothed in long white hairs below median eyes

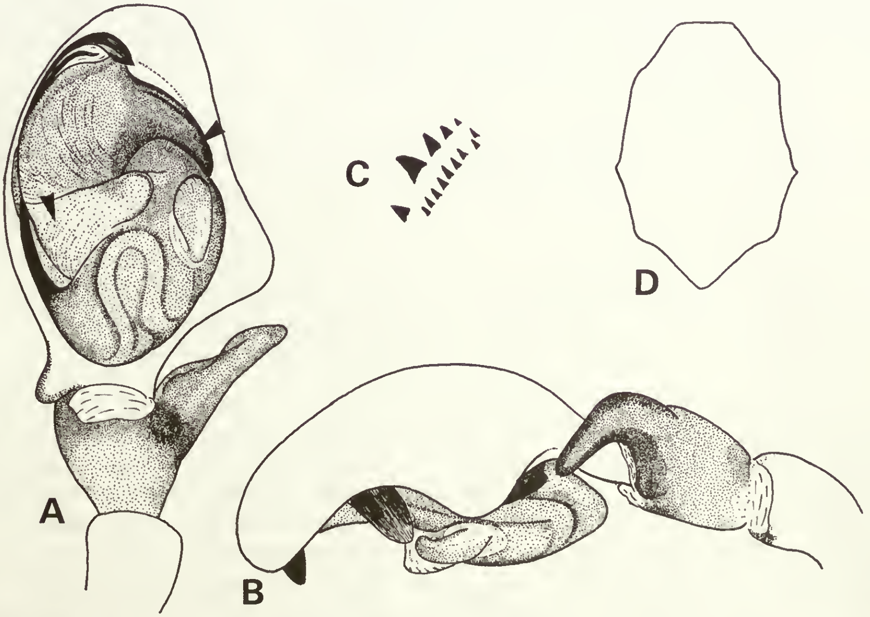

Fig. 5 *Holcolaetis vellerea* Simon, ♂ from Uganda: A, palp, ventral view; B, palp, retrolateral view; C, cheliceral teeth; D, sternum.

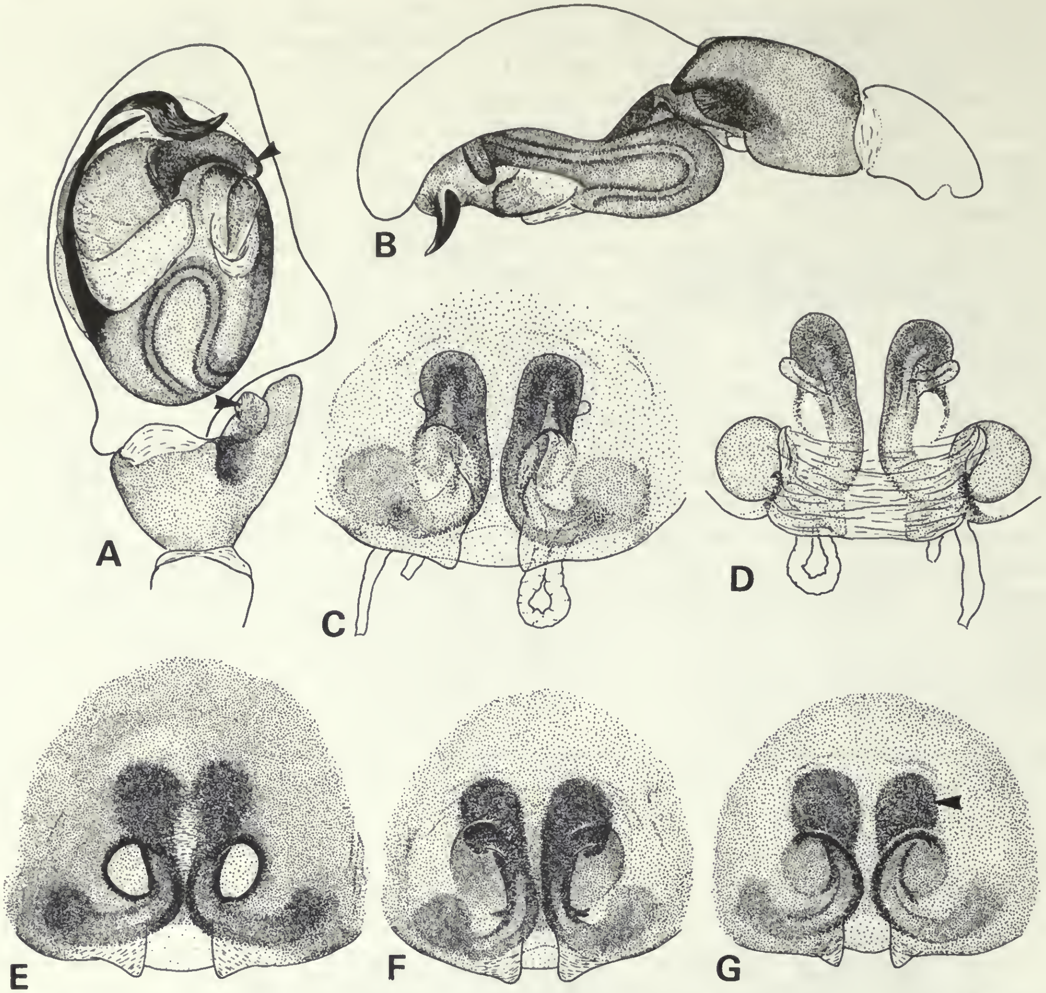

Fig. 6 *Holcolaetis zuluensis* Lawrence, ♂ from Pietermaritzburg. A, palp, ventral view; B, palp, retrolateral view. ♀ from Parfuri: C, vulva, outer view; D, vulva, inner view. ♀ type series: E–F, paralectotype, epigynes; G, lectotype, epigyne.

with amber and white ones below laterals—the white hairs in reality the start of the submarginal white haired bands. *Chelicerae:* promargin with four teeth, retromargin with eight. *Abdomen:* similar to male but with flecks and vague chevrons comprised of brown-black hairs in dentate band. *Legs:* legs I–II deep brownish orange with inside of femora, metatarsi and tarsi orange-brown; clothed in black hairs, especially dense on underside of tibiae and patellae with whitish hairs on inside of femora; also, on patellae, tibiae and inside of femora II tufts of semirecumbent white hairs; other legs light to dark brownish orange except for yellow-brown tarsi and metatarsi, the latter darker at either end particularly on legs IV; clothed in black hairs with usual scattered semirecumbent white tufts most numerous on femora and tibiae. Spination of legs I: metatarsi v 2–0–0; femora d 0–3–3, p 0–0–1. *Palps:* with base of femora lightly mottled black; clothed in white hairs and scattered light brown bristles. *Epigyne* (Fig. 4D; 16B).

Dimensions (mm): total length 11·5; carapace length 4·6, breadth 3·54, height 1·6; abdomen length 7·2; eyes, anterior row 2·4, middle row 2·38, posterior row 2·48; quadrangle length 1·8 (39% of carapace length). *Ratios:* AM : AL : PM : PL :: 18 : 9 : 7 : 9; AL–PM–P-L :: 9–13; AM : CL :: 18 : ca. 3.

Variation. Male total length varies from 6·6 to 10·2 mm, carapace length 3·4–4·6 mm, 10 specimens; female total length 9·4–13·0 mm, carapace length 4·0–5·5 mm, 10 specimens.

In males the eye region and carapace margins are sometimes heavily tinged black, the development of the retrolateral tibial apophysis also varies, but not to the extent of raising doubts in respect of identification. In females the epigynes show wide differences in appearance and are often plugged; figure 4D shows the kind of epigyne most frequently encountered, other forms are not uncommon.

Distribution. Angola; Cameroon; Ivory Coast; Kenya; North Yemen; Rwanda; São Thomé; Uganda; Zaire.

Material examined. **Angola:** Cuito, Luimbale, under eucalyptus bark, 1♀, 9.ix.1949, *A. de Barros Machado*, Ang. 1820.3. **Cameroon:** River Ja, 1♀, *G. L. Bates*, purchased off Rosenburg, (BMNH); Edea, 1♂, [holotype of *H. camerunensis*] Roewer coll., RII/9742/819 (FS, Frankfurt am Main). **Ivory Coast:** environs of Kotiessou, R. Bandama, 1♂, 1♀, 19–20.iv.1952, *J. Jezequel*, RR.28, (MNHN, Paris). **Kenya:** *J. & F. Murphy*: Kakamega Forest, 1♀, 12.viii.1972; Nairobi, Muthaiga golf course, on gum trees, 3♀♀, ix.1972; Kitale, on banana plant, 1♂, 22.vii.1974; Lake Hannington, southern end, from tree, 1♀, 2.viii.1974, (Murphy, private coll.). **North Yemen:** Wadi Suque, under peeling bark of banana tree, 1400 m, 1♀, v.1978, *H. Haig-Thomas*, (BMNH). **Rwanda:** Butare, P. Nyaluqaka: 1♂, 1♀, vi–vii.1971, MT. 140.713. 140.689; 2♂♂, II–III.1971, MT. 139. 090; 1♀, vi. 1971, MT. 139.162; Butare, *R. Kiss*, vi.1971, 1♀, MT. 141.196. 1♀, MT. 141.191; Environs Lake Ihema, *R. Kiss*, 14–18.vii.1969, 2♀♀, MT. 136.316, 1♂, MT. 136.299. (MRAC, Tervuren). **São Thomé:** Ribeira Palma, lectotype ♀, *L. Fea*, (MNHN, Paris, 23125). **Uganda:** Entebbe, 2♂♂, *E. Degen*, (BMNH. 1906.3.28.58–360, part). **Zaire:** Poko, [holotype ♂ of *H. vidua*, (AMNH, New York); Kivu, Irangi, 2♀♀, vi.1969, *S. Orts*, MT. 136.166; Tshuapa, Boende, 1♀, x.1969, *J. Hauwaerts*, MT. 136.145; Flandria, 1♀, *R. P. Hulstaert*, MT. 12056; Kutshuuree, iii.1938, 1♀, *J. Ghesquière*, MT. 1346, (MRAC, Tervuren).

Note. Dyals description of *H. vidua* (Dyal, 1935) does not appear to fit this species, in particular 'First pair of legs are thick, and reddish brown, patellae are longer than is usually the case in spiders, tibiae are short and swollen and tarsi are short and slender'. The record from Pakistan has therefore not been included in the distribution list.

Holcolaetis zuluensis Lawrence

(Figs 6, 16C)

Holcolaetis zuluensis Lawrence, 1937: 255. ♀ LECTOTYPE, 2♀♀ PARALECTOTYPES (here designated) South Africa (NM. Pietermaritzburg) [examined]. Roewer, 1954: 937; 1965: 28. Bonnet, 1957: 2223. Prószyński, 1971: 418. Clark, 1974: 16. Cutler, 1976: 132.

[*H. xerampelina*: Lessert, 1925*a*: 432, 433; 1925*b*: 342; 1927: 427. Roewer, 1965: 24. Misidentification].

Remarks.The majority of references to *H. xerampelina* Simon almost certainly refer to *H. zuluensis* Lawrence, see remarks p. 254.

Diagnosis. Close to *H. vellerea*, but easily separated by the sinuous tip of the functional conductor and presence of flanges on the palpal retrolateral tibial apophyses in males (Fig. 6A). Females are distinguished by the presence of dark patches anterior to the rounded depressions surrounding the copulatory openings (Figs 6E–G).

Female lectotype, in good condition. *Carapace:* profile typical of genus; dark reddish brown with blackened iridescent eye region and a broad pale orange-brown thoracic band tapering towards posterior margin; generally clothed in greyish hairs with whitish ones in eye region and thoracic band; also, on margins and submargins thin bands of white hairs, the latter contiguous with and becoming broader towards clypeus. *Eyes:* laterals with black surrounds; fringed by whitish and golden hairs. *Clypeus:* densely clothed in long buff hairs. *Chelicerae:* dark reddish orange, basal part of facies clothed in buff hairs overlayered by clypeal setae; promargin with four teeth, retromargin with eight (six to nine in other specimens). *Maxillae:* dark reddish orange with pale yellow inner distal margins. *Labium:* dark reddish orange. *Sternum:* orange-brown with darker margins that are wider and slightly more conspicuous opposite anterior coxe; clothed in scattered fine brown hairs with whitish ones on margins. *Coxae:* first pair dark reddish orange, rest orange-brown. *Abdomen:* dorsum yellow-brown lightly tinged black, clothed in dark amber hairs with broad yellow-brown dentate band thinly clothed in pale amber hairs and scattered bristles; pustuliform field obscure; venter pale yellowish with vague longitudinal grey bands and four rows of minute spots; spinnerets pale orange-brown lightly tinged black. *Legs:* legs I dark orange-brown suffused black with paler tarsi and metatarsi, fringed ventrally with brownish hairs; legs II as I, but paler with sparser fringes; other legs orange-brown with vague blackish annuli; also, on all legs scattered transversely set patches of white hairs. Spination of legs I: femora d 0–1–9, p 0–1–1. *Palps:* yellow-brown to orange-brown distally with sooty annuli on tarsi. *Epigyne* (Fig. 6G): note inner lining of the introductory ducts appears to be displaced in lactic acid preparations (Figs 6C, D; 16C).

Dimensions (mm): total length 12·5; carapace length 4·96, breadth 3·92, height 1·84; abdomen length 7·36; eyes, anterior row 2·76, middle row 2·68, posterior row 2·76; quadrangle length 1·96 (39% of carapace length). *Ratios:* AM : AL : PM : PL :: 20 : 11 : 7 : 10·5; AL–PM–PL :: 12–15; AM : CL :: 20 : ca.3.

MALE from Pietermaritzburg, in good condition. *Carapace:* similar to female, but darker—brownish black with broad dark reddish thoracic band; clothed in black and grey hairs with golden ones in and around eye region and whitish ones on thoracic band; marginal bands as in female. *Eyes:* fringed by golden and brown hairs. *Clypeus*: black haired. *Chelicerae*: blackish red with scattered fine black hairs; promargin with five teeth, retromargin with seven. *Maxillae and labium:* reddish black the former with light yellowish inner distal margins. *Sternum:* dark orange-brown with darker margins; clothed in scattered black and marginal white hairs. *Coxae:* orange-brown first pair darkest. *Abdomen:* densely clothed in black hairs with broad central band comprised of creamy yellow hairs; pustuliform field relatively conspicuous; venter brownish black, clothed in short black hairs with vague longitudinal whitish bands laterally. *Legs:* long and slender in respect of female and also generally hirsute; legs I brown-black with dense black fringes and patches of recumbent white hairs on prolateral surface of patellae and basal prolateral face of metatarsi; legs II with orange-brown tarsi, other segments brown-black with vague paler markings, generally clothed in long black hairs forming dense fringes on lower retrolateral face of femora and patellae and venter of tibiae; also present usual scattered patches of recumbent white hairs especially on patellae and femora; other legs similar, but with less conspicuous fringes and pale metatarsi becoming blackish distally. Spination of legs I: femora d 0–6–2. *Palp:* (Fig. 6A, B).

Dimensions (mm): total length 11·2; carapace length 5·68, breadth 4·16, height 2·16; abdomen length 5·68; eyes, anterior row 3·02, middle row 2·88, posterior row 2·92; quadrangle length 2·24 (39% of carapace length). *Ratios:* AM : AL : PM : PL :: 21·5 : 12 : 8 : 11; AL–PM–PL :: 13–17; AM : CL :: 21·5 : ca. 5.

VARIATION. Male total length varies from 8·7 to 11·2 mm, carapace length 4·22–5·68 mm, five specimens; female total length 9·36–15·2 mm, carapace length 4·04–6·16 mm, 10 specimens.

Variation in the appearance of the epigyne is clearly evident from the type series (Fig. 6E–G).

DISTRIBUTION. South Africa; Tanzania.

MATERIAL EXAMINED. **South Africa:** Natal, no other data: 5♀♀, 2 juveniles, *Ch. Martin*, (MNHN, Paris. 20189); 3♀♀, (MCZ, Harvard); 1♀, (Milwaukee Museum, Milwaukee); Natal: Durban, 2♂♂, *G. P. Staunton*, (BMNH); 3♀♀, *J. F. Quekett*, (MCZ, Harvard); 1♂, 1♀, *J. F. Quekett*, (MCZ, Harvard); Otobotini, 1♀, vii.1938, (NM, Pietermaritzburg); Pietermaritzburg, 1♂, 1917, *C. Akerman*, (NM, Pietermaritzburg, 2430); Zululand, Kosi Bay, lectotype ♀, paralectotypes 2♀♀, vii.1936 (NM, Pietermaritzburg, 140); Willow Fountain, Pietermaritzburg, iv.1958, 1♂, (NM, Pietermaritzburg, 6987); Transvaal, Kruger N. P., Parfuri, 2♀♀, *H. Braak*, (BMNH). **Tanzania:** Ngare Nanyuki 1♂, 1♀, *Y. Siostedt*, (NR, Stockholm).

Holcolaetis albobarbata Simon
(Figs 7, 8, 16D)

Holcolaethis albobarbata Simon, 1909 (1910): 79. LECTOTYPE ♀, PARALECTOTYPE ♀ (here designated) Angola, (MNHN, Paris) [examined]; [*Holcolaethis*, lapsus for *Holcolaetis*].

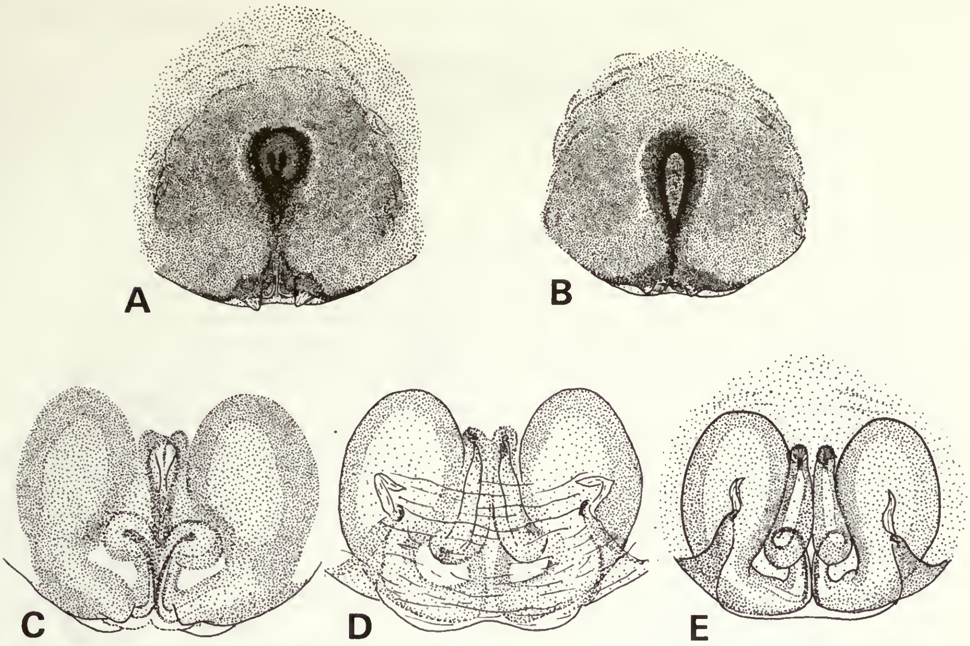

Fig. 7 *Holcolaetis albobarbata* Simon, ♀: A, lectotype epigyne; B, paralectotype epigyne; C–E, paralectotype vulva: C, outer view, connective tissue *in situe*; D, inner view, connective tissue *in situe*; E, inner view, connective tissue removed.

Holcolaetis albobarbata: Lessert, 1925*a*: 434. Roewer, 1954: 937; 1965: 25. Bonnet, 1957: 2222. Prószyński, 1971: 417. Clark, 1974: 16.
[*Holcolaethis strandi*: Caporiacco, 1941: 135, misidentification].

Remarks. The original description of *H. strandi* Caporiacco was based on a juvenile and as a consequence it is treated here as a species incertae sedis. A subsequent description (Caporiacco, 1941) based on an adult female, which has been re-examined, is clearly conspecific with *H. albobarbata.*

Roewer (1965) figured the epigyne of both *H. strandi* and *H. albobarbata,* of these, his figure of *strandi* is a poor copy of Caporiacco's original, whereas the *albarbata* [*sic*] figure does not agree with any known species of *Holcolaetis*. Clark, in correspondence, reached the same conclusion as the present author, namely that Roewer's salticid studies are crude and unreliable.

Diagnosis. Similar to *H. clarki,* but separated by the absence of well developed flanges on the palpal retrolateral tibial apophysis in males (Fig. 8B,F) and by the more or less ovate depression surrounding the copulatory openings in females (Fig. 7A,B).

Female lectotype, in poor condition. *Carapace:* profile typical of genus; dark reddish with vague broad dull orange band on thoracic part; irregularly clothed in whitish pubescence (rubbed). *Eyes:* laterals with black surrounds; fringed by whitish hairs. *Clypeus:* densely white haired. *Chelicerae:* dark reddish with short white hairs basally and scattered long pale golden ones elsewhere; promargin with six teeth, retromargin with seven. *Maxillae and labium:* reddish orange with inner distal margins of maxillae and labial tip whitish yellow. *Sternum:* pale yellowish orange with darker margins; thinly clothed in fine pale yellowish hairs. *Coxae:* first pair light reddish orange, others yellowish orange. *Abdomen:* damaged and badly rubbed; greyish white with patches of whitish and amber mottling clothed in amber and light golden hairs, basic markings characteristic of genus. *Legs:* legs I dark reddish orange with fringe of amber hairs on venter of tibiae and patellae; other legs generally pale yellowish with dark orange markings forming vague annuli on tibiae III–IV and metatarsi IV. Spination of legs I: femora d 0–2–2, p 0–1–2.

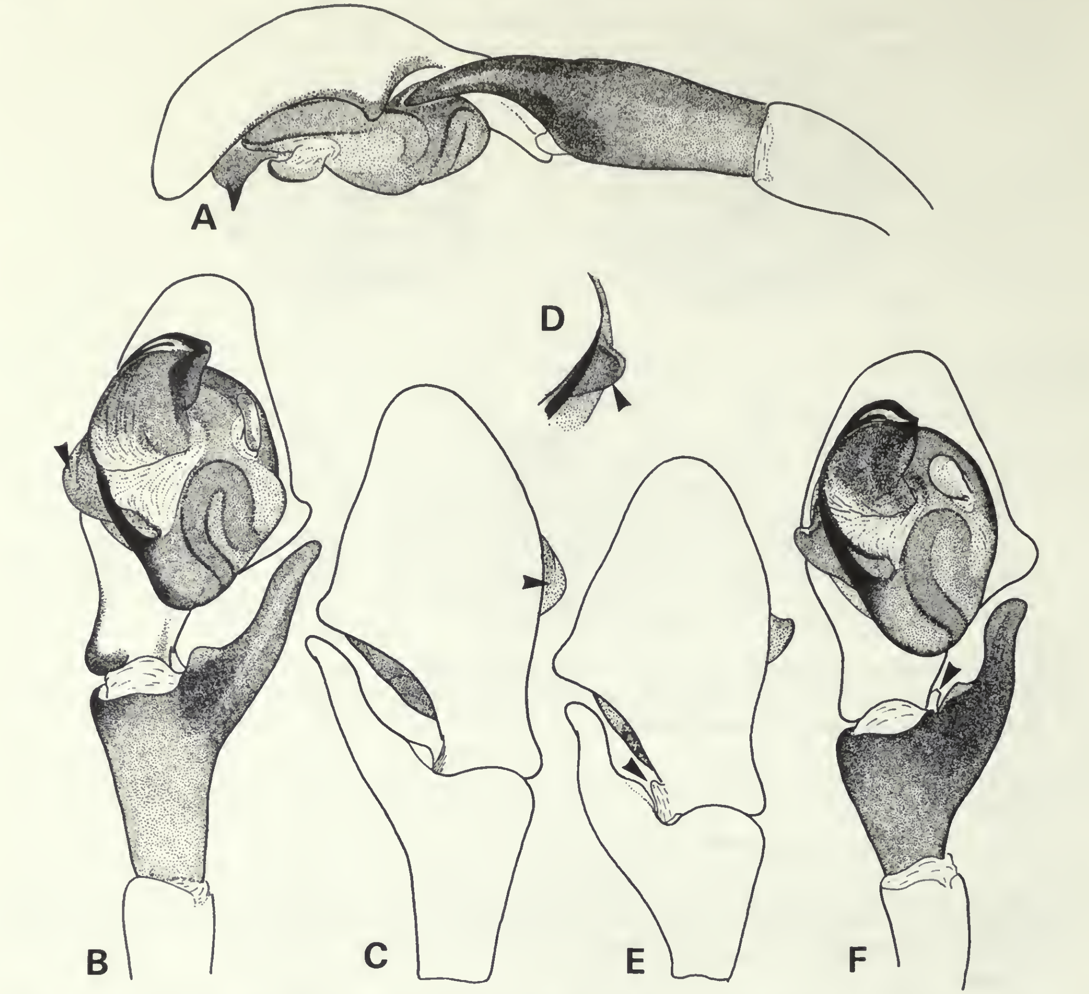

Fig. 8 *Holcolaetis albobarbata* Simon, ♂: A–C, left palp of Cameroon specimen; A, retrolateral view; B, ventral view; C, dorsal view—cymbial spur lacking. D–F, palps of Ugandan specimen: D, tegular flange of right palp, ventral view; E, left palp, dorsal view—cymbial spur present, arrowed; F, left palp, ventral view, cymbial spur, arrowed.

Palp: femora and patellae pale yellowish orange, remaining segments dark reddish; clothed in white and golden hairs. *Epigyne* (Fig. 7A).

Dimensions (mm): total length ca. 14·0; carapace length 5·28, breadth 3·84, height 2·0; abdomen length ca. 8·8; eyes, anterior row 2·9, middle row 2·88, posterior row 2·96; quadrangle length 2·08 (39% of carapace length). *Ratios:* AM : AL : PM : PL :: 21·5 : 12 : 8 : 12; AL–PM–PL :: 14–18; AM : Cl :: 21·5 : ca.4·5.

MALE from Cameroon, in fair condition. *Carapace:* profile typical of genus; dark orange-brown tinged black especially in eye region; rubbed. *Eyes:* laterals with black surrounds. *Clypeus:* clothed in pale grey/brown hairs. *Chelicerae:* orange-brown faintly tinged black; rubbed; promargin with six teeth, retromargin with nine. *Maxillae:* orange-brown with whitish yellow inner margins. *Labium*: dark orange-brown. *Sternum:* yellow-brown with darker margins. *Coxae:* first pair orange-brown, rest paler. *Abdomen:* rubbed; pale yellow lightly mottled black on sides, basic markings typical of genus; spinnerets yellow-brown tinged black. *Legs:* with pale golden fringes on venter of patellae and tibiae of legs I; generally yellow-brown with apices of metatarsi blackish, particularly on legs III–IV. Spination of legs I: femora d 0–2–3, p 0–2–2. *Palp* (Fig. 8A–C).

Dimensions (mm): total length 10·24; carapace length 4·44, breadth 3·12, height 1·68; abdomen length 5·76; eyes, anterior row 2·52, middle row 2·44, posterior row 2·48; quadrangle length 1·9 (42% of carapace length). *Ratios:* AM : AL : PM : PL :: 20 : 10 : 7 : 10; AL–PM–PL :: 11–14·5; AM : CL :: 20 : 2.

VARIATION. Males vary from 9·84 to 10·8 mm total length, 4·16–4·56 mm carapace length, three specimens; female total length 12·5–14·0 mm, carapace length 4·88–5·02 mm, three specimens.

In males the tegular flange is sometimes damaged (Fig. 8F) the profile of the retrolateral tibial apophysis and functional conductor is variable; also, the peg-like spur on the base of the cymbium (arrowed, Fig. 8E,F) is apparently lacking in some palps. In females the margins of the orifice leading into the copulatory openings may be ill-defined and obscured by detritus or plugged.

DISTRIBUTION. Angola; Cameroon; Uganda; Zaire.

MATERIAL EXAMINED. **Angola:** Landana, lectotype ♀, paralectotype ♀, (MNHN, Paris. 20206). **Cameroon:** Benito River, 1♂, *G. L. Bates,* (BMNH. 1898.5.5.126–137 part); Kribi, *G. L. Bates,* (BMNH. 1907.6.27.1–82 part). **Uganda:** *G. O. Evans,* Ruwenzori Expedition, 1♂, beating vegetation, chiefly grassland on margin of dense forest, 10 miles NNE Bundibugyo, 26.viii.1952, (BMNH). **Zaire:** Kisantu, 1♀, *P. Vanderyst,* 1927, MT. 12059 (MRAC, Tervuren).

NOTE. The male described above probably belongs here, but this should be confirmed since there is little to choose between the male specimens listed above and the males assigned to *H. clarki* sp.n. There is an overlap in their distribution and they may have been mismatched.

Holcolaetis clarki sp. n.

(Figs 9, 10, 16E)

DIAGNOSIS. Close to *H. albobarbata,* but separated by the presence of well-developed flanges on the retrolateral tibial apophysis in males (Fig. 10A, D) and by rounded depressions surrounding the copulatory openings in females (Fig. 9C, D).

FEMALE HOLOTYPE, in good condition. *Carapace* (Fig. 9A, B): chestnut brown tinged black in eye region with irregular light orange-brown margins and central band on thoracic part; eye region clothed in greyish and dull amber hairs with whitish grey ones on thoracic band and dark brownish ones thinly interspersed with white hairs on the sides, the brown hairs grading to black adjacent to marginal bands which are clothed in white hairs. *Eyes:* laterals with black surrounds; fringed in light brownish and dull amber hairs with white ones between anterior medians and on lower rims of anterior laterals. *Clypeus:* clothed in some black and amber hairs with white ones in lower space between anterior median eyes and below anterior laterals—the origin of the white marginal bands; also, a few long white scattered hairs on lower margin. *Chelicerae:* orange-brown lightly tinged black; shiny; clothed in short white and black hairs basally with long fine brownish ones distally; teeth not examined. *Maxillae and labium:* orange-brown with inner distal margins of maxillae and labial tip whitish yellow. *Sternum* (Fig. 10E): light yellow-brown with darker margins; shiny; thinly clothed in whitish and pale brown hairs. *Coxae:* pale yellow-brown. *Abdomen:* generally pale yellow with broad dorsal dentate band clothed in pale brownish lanceolate hairs with dark brownish and black hairs laterally, the latter forming flecks on upper sides; venter flecked and spotted with brown-black hairs; also, from epigyne to spinnerets two vague and rather scanty bands of greyish lanceolate hairs; spinnerets dark yellow-brown tinged with some black. *Palps:* femora and patellae whitish yellow, tibiae and tarsi light to dark orange-brown; clothed in long white hairs. *Legs:* legs I femora yellow-brown with sooty markings, patellae and tibiae brown with lighter patches, metatarsi and tarsi light orange-brown with

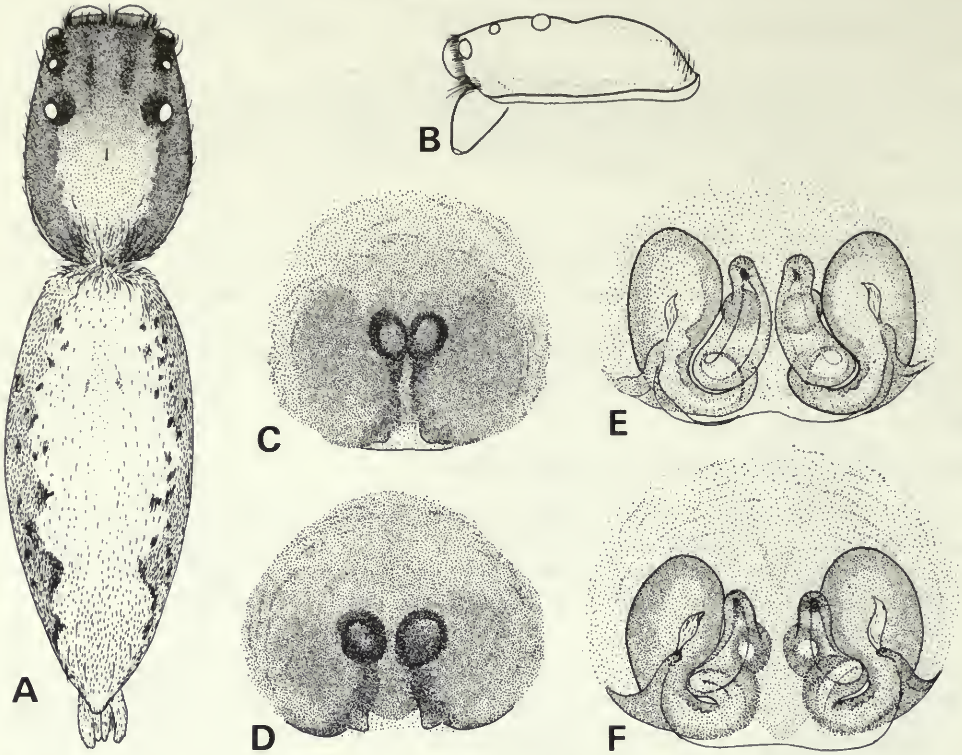

Fig. 9 *Holcolaetis clarki* sp. n., holotype ♀: A, dorsal view; B, carapace, lateral view; C, epigyne. D, epigyne, paratype from Cameroon; E, vulva, inner view—Cameroon paratype; F, vulva, inner view—Ghanain paratype.

apices of former segment sooty; generally clothed in blackish hairs forming scanty ventral fringes on tibiae and patellae; also, scattered white hairs especially on femora forming sparse recumbent tufts; other legs generally light yellow-brown with blackish markings. Spination of legs I: femora d 0–2–3, p 0–1–1. *Epigyne* (Fig. 9C).

Dimensions (mm): total length 12·3; carapace length 4·4, breadth 3·08, height 1·64; abdomen length 7·84; eyes, anterior row 2·44, middle row 2·4, posterior row 2·48; quadrangle length 1·92 (43% of carapace length). *Ratios:* AM : AL : PM : PL :: 19 : 10 : 7 : 11; AL–PM–PL :: 11–14; AM : CL :: 19 : 5.

MALE PARATYPE, in poor condition. *Carapace:* profile typical of genus; dark orange-brown tinged black in eye region with vague paler band on thoracic part and indistinct light marginal bands; largely rubbed, otherwise clothed in grey/pale amber hairs with white ones on margins. *Eyes:* laterals with black surrounds; fringed by whitish hairs with dull amber ones around lower rims of anterior row. *Chelicerae:* dark brownish orange lightly tinged black with scattering of dark amber hairs basally; otherwise rubbed; promargin with seven teeth, retromargin with eight. *Clypeus:* clothed in amber hairs. *Maxillae:* orange-brown with paler distal margins. *Labium:* orange-brown tinged black. *Sternum* (Fig. 10F): pale yellow-brown with darker margins; shiny. *Coxae:* pale yellow-brown; shiny. *Abdomen:* rubbed; a broad pale yellow dentate band dorsally with blackish mottling on sides; ventrally a vague broad longitudinal grey band containing two darker lines. *Legs:* legs I–II orange-brown tinged black, first pair with remnants of ventral amber fringes; other legs yellow-brown with blackish markings. Spination of legs I: femora p 0–1–1; d 0–2–2. *Palp* (Fig. 10A–C).

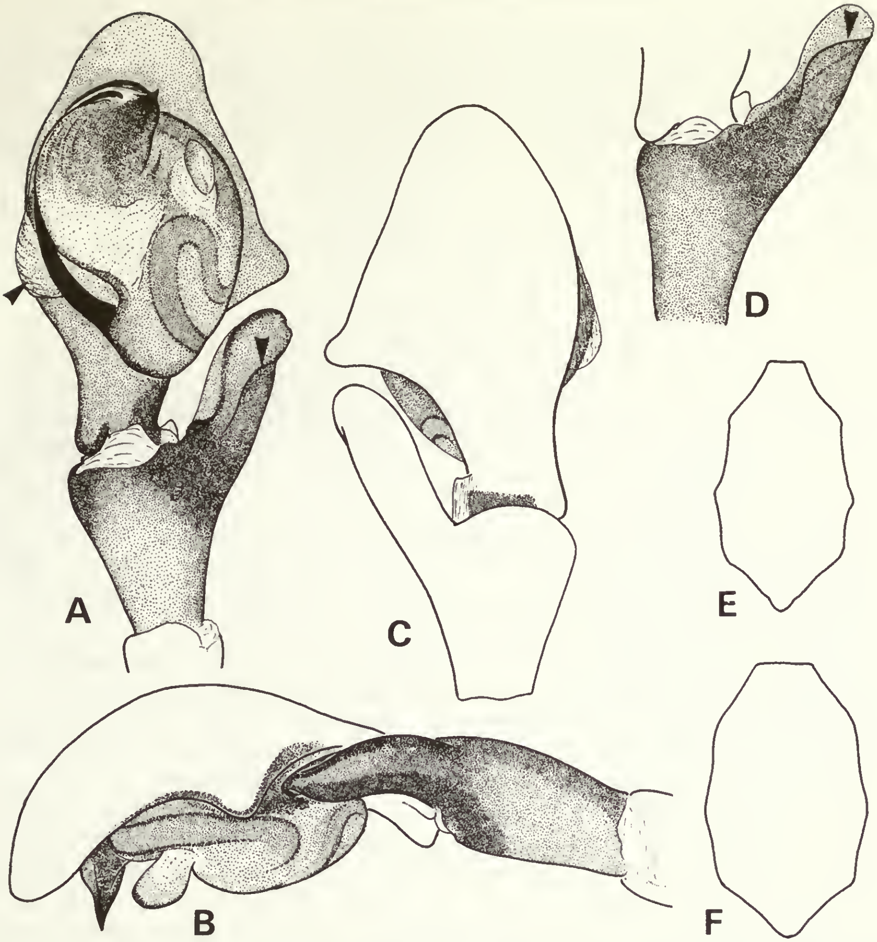

Fig. 10. *Holcolaetis clarki* sp. n., paratype ♂ from Cameroon 'no other data': A, palp, ventral view; B, palp, retrolateral view; C, palp, dorsal view; F, sternum. D, ♂ from Cameroon, Kribi River, palpal tibia ventral view. E, holotype ♀, sternum.

Dimensions (mm); total length 7·44; carapace length 3·24, breadth 2·24, height 1·24; abdomen length 4·24; eyes, anterior row 1·9, middle row 1·88, posterior row 1·94; quadrangle length 1·4 (43% of carapace length). *Ratios:* AM : AL : PM : PL :: 15·5 : 8·5 : 5 : 8; AL–PM–PL :: 9–11; AM : CL :: 15·5 : 3.

VARIATION. Another male measures 8·8 mm total length, 4·32 mm carapace length; females vary from 11·3–13·6 mm total length, 3·9–5·36 mm carapace length, seven specimens.

Females that have been preserved for longer periods than the specimen described above are somewhat redder in colour and the patterns are less distinctive. The vulvae also vary in appearance, due probably to differences in the size and disposition of the introductory ducts. In one female from Angola the clypeus is clothed in white hairs. In males the palp of a relatively large specimen has more pronounced flanges on the retrolateral tibial apophysis (Fig. 10D), possibly an allometric growth character.

DISTRIBUTION. Angola; Cameroon; Ghana; Zaire.

MATERIAL EXAMINED. **Angola:** environs of Dundo, forest zone, R. Luachimo, under bark, ♀ paratype, 6.vii.1948, *A. de Barros Machado,* Ang. 829.3. **Cameroon:** Edea, ♀ paratype, Roewer Coll. RII/9270/591, (FS, Frankfurt am Main); 1♂, 1♀, paratypes *G. L. Bates*, no other data; Efulen, ♀, paratype, *G. L. Bates*, Kribi River, 25 miles from coast, ♂, paratype, *G. L. Bates*, (BMNH. 1984.2.24.1.4). **Ghana:** Bibianaba, 1♀, paratype, 29.x.1911, *H. G. Spurrell*, (BMNH. 1984.2.24.5). **Zaire:** Kivu, forêt de Visiki, holotype ♀, 27.xii.1971, *R. P. M. Lejeune*, MT. 140905; Kivu, confluent Semliki-Djuma, ♀ paratype, *R. P. M. Lejeune*, MT. 135.625; Mongbwalu, 2♀♀ paratypes, vii.1973, *Mme Scheitz*, MT. 1575–1578, (MRAC, Tervuren).

REMARK. See note. p. 260.

ETYMOLOGY. This species is named after the late Mr D. J. Clark, British Museum (Natural History) who had clearly solved many of the problems associated with this genus.

Species incertae sedis

Holcolaetis strandi Caporiacco

This species was described from a juvenile female and to judge from Caporiacco's measurements, the specimen was several moults from adulthood. The holotype has not been examined and the species cannot at the present time be positively identified from the original description.

Genus *SONOITA* Peckham & Peckham

Sonoita Peckham & Peckham, 1903: 183. Type species *Sonoita lightfootii* Peckham & Peckham, by original designation and monotypy. Waterhouse, 1912: 277. Petrunkevitch, 1928: 182. Neave, 1940, iv: 224. Roewer, 1954: 937; 1965: 19. Bonnet, 1958: 4019. Prószyński, 1971: 475. Cutler, 1976: 134. Wanless, 1982: 264; 1984*a*: 138.

DEFINITION. Spiders of medium size, i.e. total length between 4·0–8·0 mm. Sexual dimorphism not marked, only known species with strong ventral fringes on tibiae of legs I.

Carapace: moderately high, longer than broad, widest at about level between coxae II–III; fovea moderately long, sulciform, apex at level of posterior margins of posterior lateral eyes. *Eyes:* with moderately strong lenses set on low tubercles; anteriors closely set, subequally spaced with apices procurved in frontal view; anterior laterals more than half diameter of anterior medians; posterior medians relatively large, positioned closer to and just outside optical axis of anterior laterals; posterior laterals almost as large as anterior laterals and positioned well inside of carapace margins when viewed from above; posterior ocular quadrangle broader than long and wider behind; entire quadrangle occupying between 46–49% of carapace length. *Clypeus:* low. *Chelicerae:* moderately robust; facies more bulbous in females; fang moderately strong and curved; promargin with three to five teeth, retromargin with five or six. *Maxillae:* long and parallel with rounded outer distal margins. *Labium:* slightly longer than broad and about half maxillae length. *Sternum:* elongate scutiform in female, evidently similar in males, but partly obscured by coxae in available specimens. *Coxae:* fourth pair noticeably larger than I–III. *Abdomen:* elongate ovoid, sometimes marked with subcutaneous quanin (?) artifact of preservation; basic pattern, of only unrubbed specimen, comprised of paler longitudinal dorsal band containing chevrons posteriorly and flanked by flecks on either side; pustuliform field comprised of scattered pustuliform organs obscured by setae; spinnerets moderately long, posteriors and anteriors unequally robust, medians shorter and more slender; tracheal system not examined, insufficient material, spiracle presumably an indistinct slit near base of anterior spinnerets; former position of colulus represented by scanty group of setae. *Legs:* moderately long and slender with strong ventral fringes on tibiae and retroventral surface of femoral apices; spines moderately strong and numerous: in male present on metatarsi, tibiae, patellae and femora of all legs, in females similar, but legs I–II with femoral spines only; claws smooth or pectinate; tufts present; scopulae absent.

Epigyne: small and structurally similar to *Holcolaetis*; posterior margin with delicate flanges; copulatory openings somewhat disc-like, but indistinct; introductory ducts broad and looped; glandular appendices not evident; spermathecae apparently subovoid, but precise form uncertain as they blend and appear to fuse with the introductory ducts (Figs 11K, L); fertilisation ducts slender, leaf-like and apparently supported as in *Holcolaetis*.

Male palps: essentially as in *Holcolaetis* except retrolateral tibial apophysis broad and fan-like; expanded palps not examined—insufficient material.

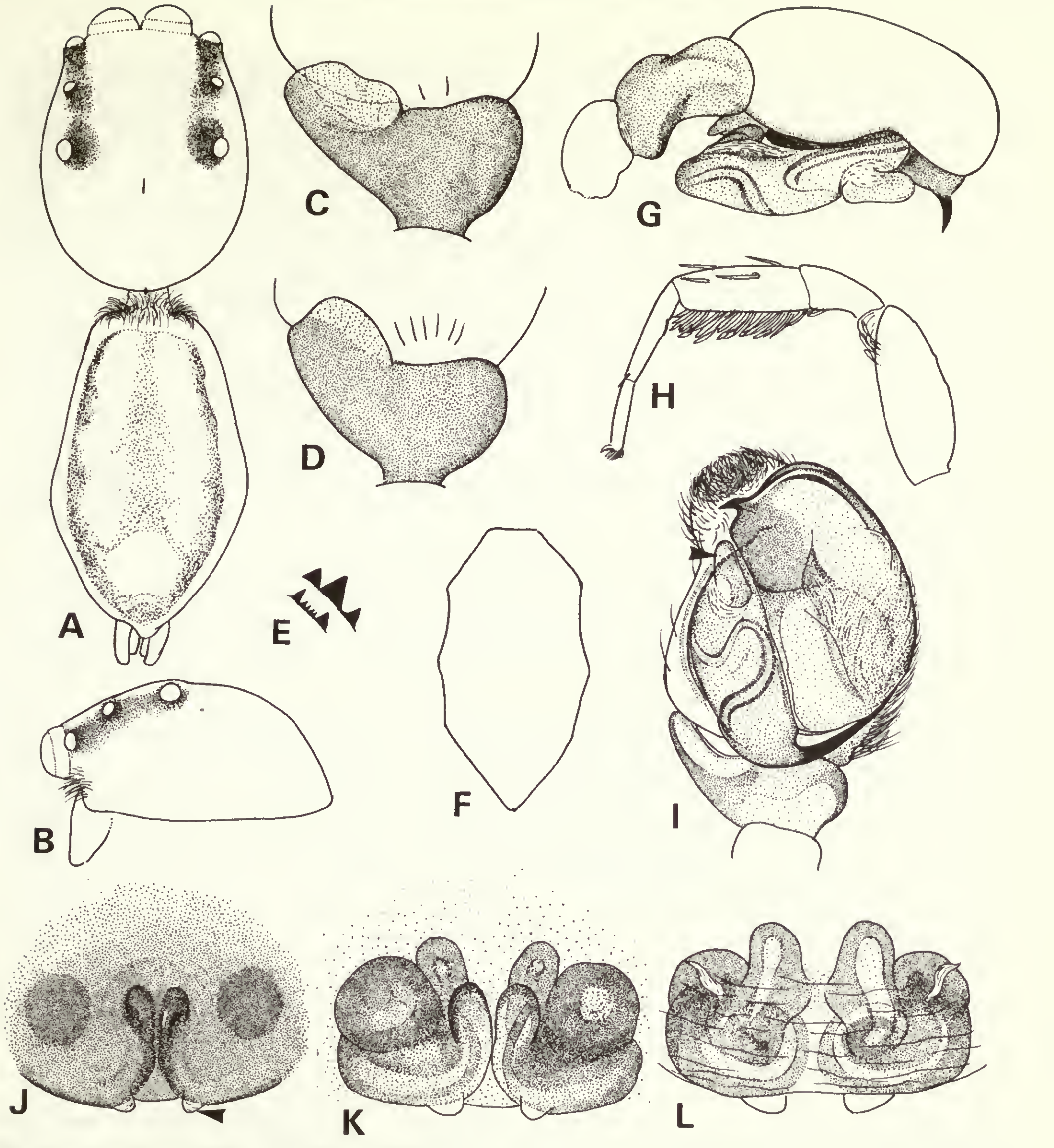

Fig. 11 *Sonoita lightfooti* Peckham & Peckham, holotype ♂: A, dorsal; B, carapace, lateral view; C, palpal tibia, dorsal view; E, cheliceral teeth; G, palp, retrolateral view; H, leg I; I, palp, ventral view. ♀ from Ivory Coast: F, sternum; J, epigyne; K, vulva, outer view; L, vulva, inner view.

Diagnosis. From *Holcolaetis* by the moderately high carapace and from all other salticids by the combination of large posterior median eyes, bowl-like median apophysis in males (arrowed, Fig. 11I) and translucent epigynal flanges in females (arrowed, Fig. 11J).

Affinities. See discussion on *Holcolaetis*.

Sonoita lightfooti Peckham & Peckham
(Figs 11, 13, 14, 16F)

Sonoita lightfootii Peckham & Peckham, 1903: 184. Holotype ♂, Cape Colony, (MCZ, Harvard) [examined]. Roewer, 1954: 937; 1965: 20. Cutler, 1976: 134.
S. lightfooti: Bonnet, 1958: 4091. Prószyński, 1971: 75.

DIAGNOSIS. As generic diagnosis.

MALE HOLOTYPE, in poor condition. *Carapace* (Fig. 11A, B): dark brown lightly tinged with some black in eye region; rubbed, except for scattered fine whitish/pale amber hairs on sides. *Eyes:* laterals with black surrounds; fringed by whitish hairs. *Clypeus:* clothed in dirty white hairs. *Chelicerae:* brownish with paler inner distal margins; basally clothed in whitish hairs with scattered amber hairs elsewhere; promargin with three teeth, retromargin with two. *Maxillae and labium:* brownish tinged black with paler tips. *Sternum:* brownish tinged black; shiny. *Coxae:* brownish. *Abdomen:* contents shrunken, original pattern indistinct generally blackish with light brown markings and tuft of amber and whitish hairs anteriorly; spinnerets light brown tinged with some black. *Legs:* moderately long and slender; legs I (Fig. 11H) dark amber tinged black except for tarsi and metatarsi which are yellow-brown; tibiae I with dense ventral fringe of amber spatulate setae; other legs, excluding missing second pair, generally yellow-brown with vague blackish mottling and indistinct annuli on apices of metatarsi; spines moderately strong and numerous. Spination of legs I: metatarsi v 2–0–1, d 1–0–2; tibiae d 3–1–2; patellae p 0–1–0, r 0–1–0; femora d 0–2–3, d 0–2–3, p 0–0–1. *Palp* (Fig. 11C, G).

Dimensions (mm): total length 4·5; carapace length 2·08, breadth 1·56, height 1·08; abdomen length 2·44; eyes, anterior row 1·2, middle row 1·22, posterior row 1·32; quadrangle length 0·96 (46% of carapace length). *Ratios:* AM : AL : PM : PL :: 9 : 5 : 3·5 : 5; AL–PM–PL :: 6–9; AM : CL :: 9 : ??.

FEMALE from Ivory Coast, in fair condition, formerly undescribed. *Carapace:* profile as in male; orange-brown lightly tinged with some black especially in eye region; clothed in rather coarse white hairs with pale golden ones forming vague longitudinal bands in eye area. *Eyes:* laterals with black surrounds; fringed by white hairs with pale golden ones on upper rims of anterior medians. *Clypeus*: covered in long white hairs. *Chelicerae:* orange-brown; shiny; thinly clothed in white and fine pale brown hairs; pro- and retromargin with five teeth. *Maxillae:* pale yellow-brown with whitish inner distal margins. *Labium:* yellow-brown lightly tinged black with whitish tip. *Sternum* (Fig. 11F): light orange-brown suffused black; shiny thinly clothed in coarse white hairs with fine pale hairs centrally. *Coxae:* IV clearly largest; pale yellow-brown; shiny. *Abdomen:* greyish yellow with yellow subcutaneous quanin dorsally; clothed above in white and scattered dark amber hairs forming flecks on sides—basic pattern rather as in *Holcolaetis*; venter pale yellow with broad blackish band containing four rows of pale spots. *Legs:* legs I with strong fringes of grey/black lanceolate hairs on underside of tibiae and retroventral surface of femoral apices; general colouration of tarsi and metatarsi yellow-brown, tibiae, patellae and femora orange-brown tinged black; other legs yellow-brown with blackish markings forming irregular annuli; clothed in scattered white hairs. Spination of legs I: femora p 0–0–1, d 0–2–2. *Palps:* light yellow-brown with sooty markings. *Epigyne* (Figs 11J–L; 16F).

Dimensions (mm); total length ca. 5·6 (bent); carapace length 2·16, breadth 1·64, height 1·12, abdomen length 3·4; eyes, anterior row 1·24. middle row, 1·2, posterior row 1·32; quadrangle length 1·06 (49% of carapace length). *Ratios:* AM : AL : PM : PL :: 9·5 : 5 : 3 : 5; AL–PM–PL :: 7–9; AM : CL :: 9·5 : 3.

VARIATION. Another male measures ca. 4·05 mm total length 1·96 mm carapace length; whereas a damaged female measures ca. 5·5 mm total length, 2·28 mm carapace length.

The abdominal pattern of a second Ivory Coast female differs from that described above in that it lacks conspicuous yellow quanin and as such resembles the holotype male. In males there are differences in the shape of the retrolateral tibial apophyses (Fig. 11C, D) which are not considered to be significant in view of overall similarities in other characters.

DISTRIBUTION. Ivory Coast; South Africa.

MATERIAL EXAMINED. **Ivory Coast:** River Bandama, environs Kotiessou, from a tree *Pilostigma thonningii, Lamotte* coll., PNB 179, 1♂; PNB 146, 2♀♀, PNB 174, i juv. (MNHN, Paris). **South Africa:** Cape Colony, holotype ♂, *Peckham coll.,* (MCZ, Harvard).

REMARKS. The pustuliform fields could not be examined properly because of damage and

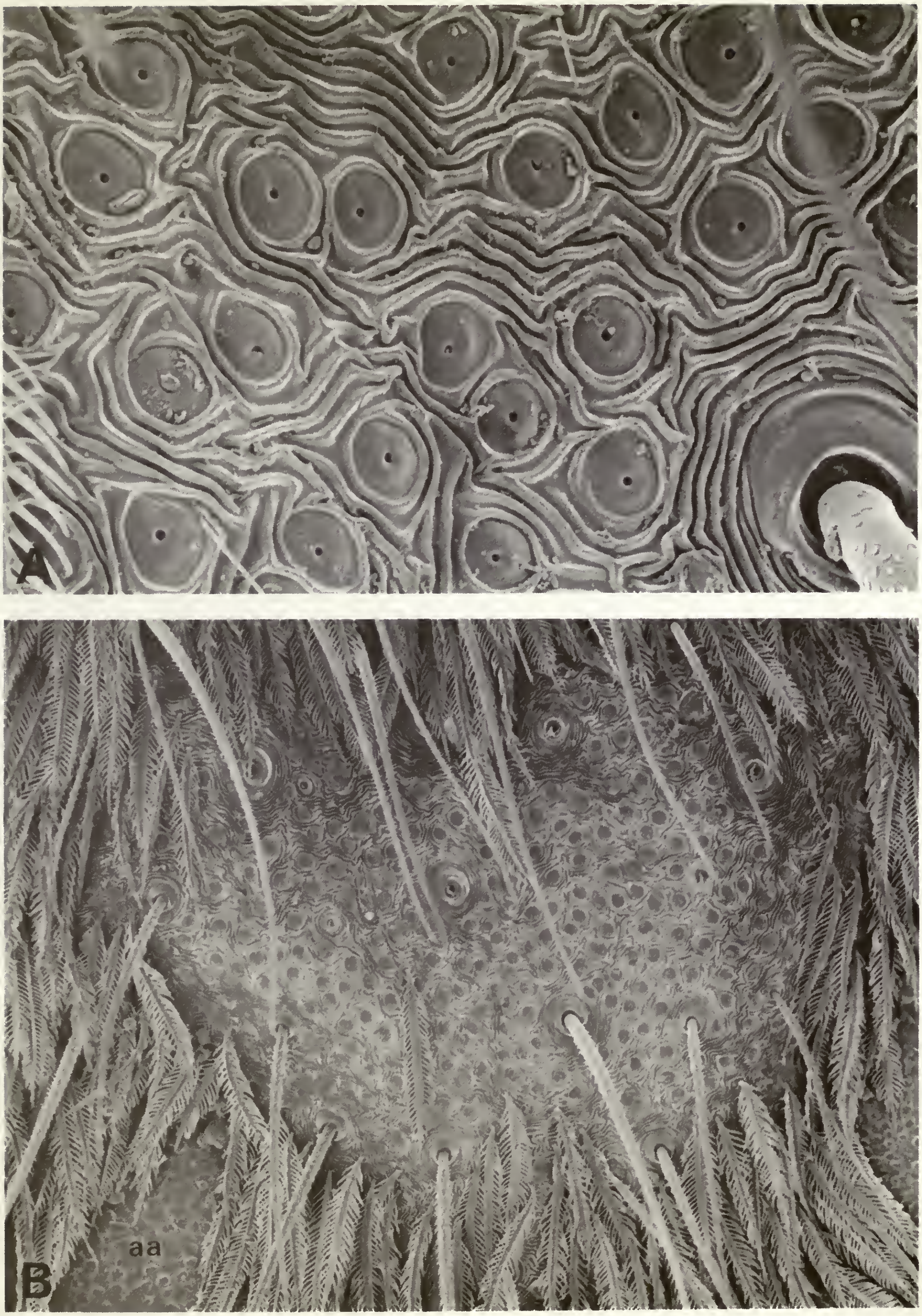

Fig. 12 *Holcolaetis vellerea* Simon, ♀: dorsal surface of abdomen showing pustuliform field: A, × 900; B, × 168.

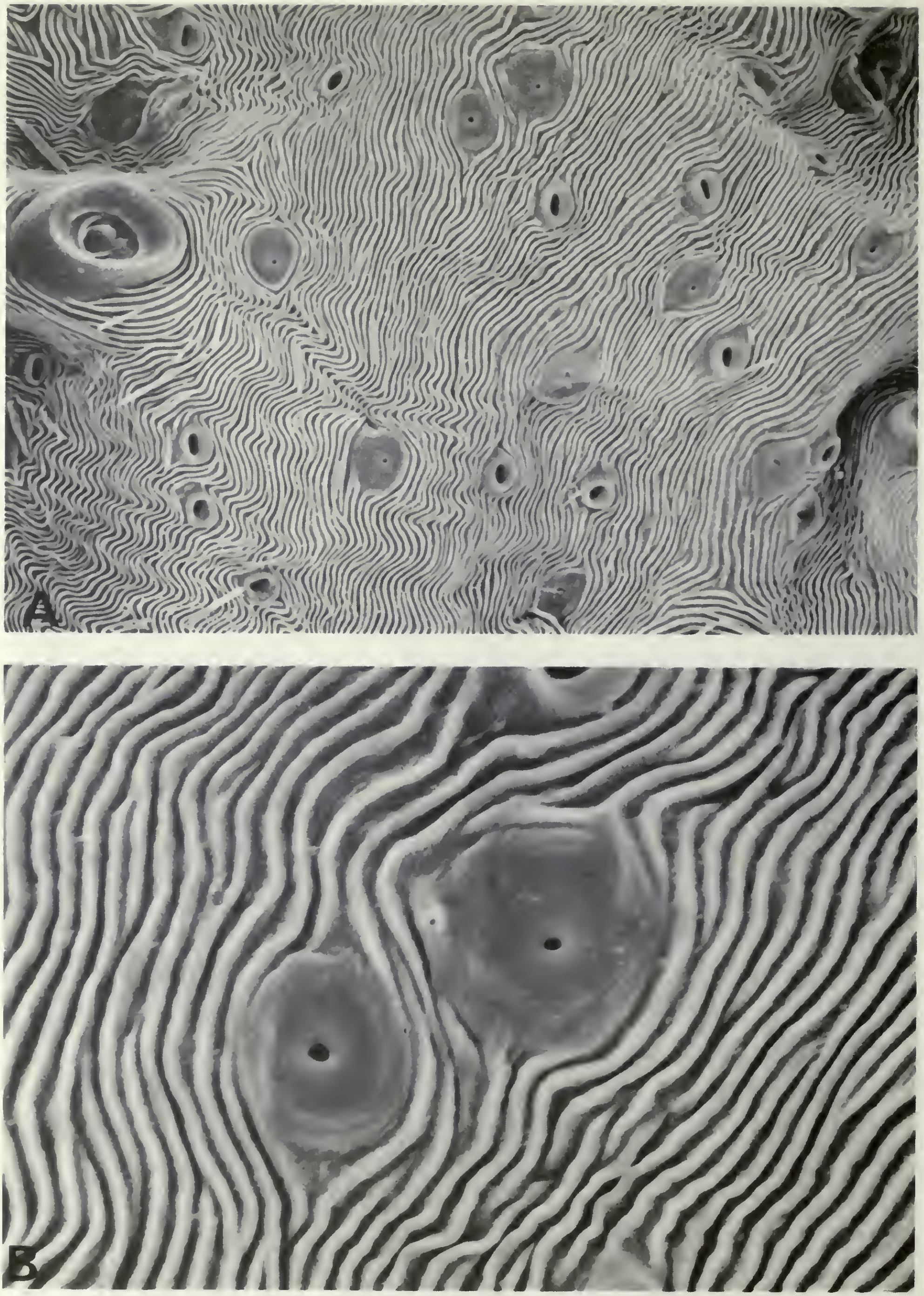

Fig. 13 *Sonoita lightfooti* Peckham & Peckham, subadult ♀ pustuliform organs: A, × 1300; B, × 4500.

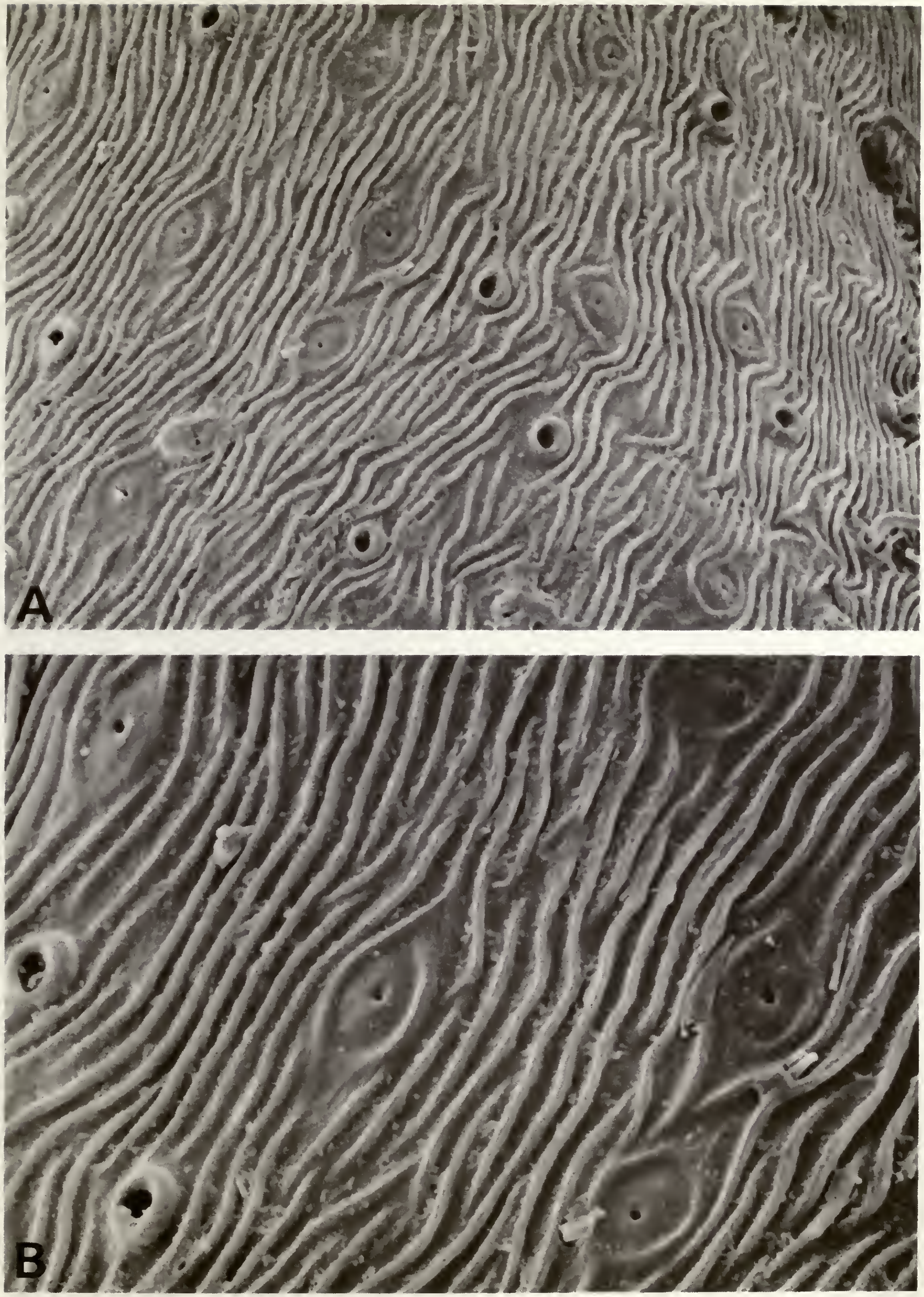

Fig. 14 *Sonoita lightfooti* Peckham & Peckham, ♀ pustuliform organs: A, × 1400; B, × 3000.

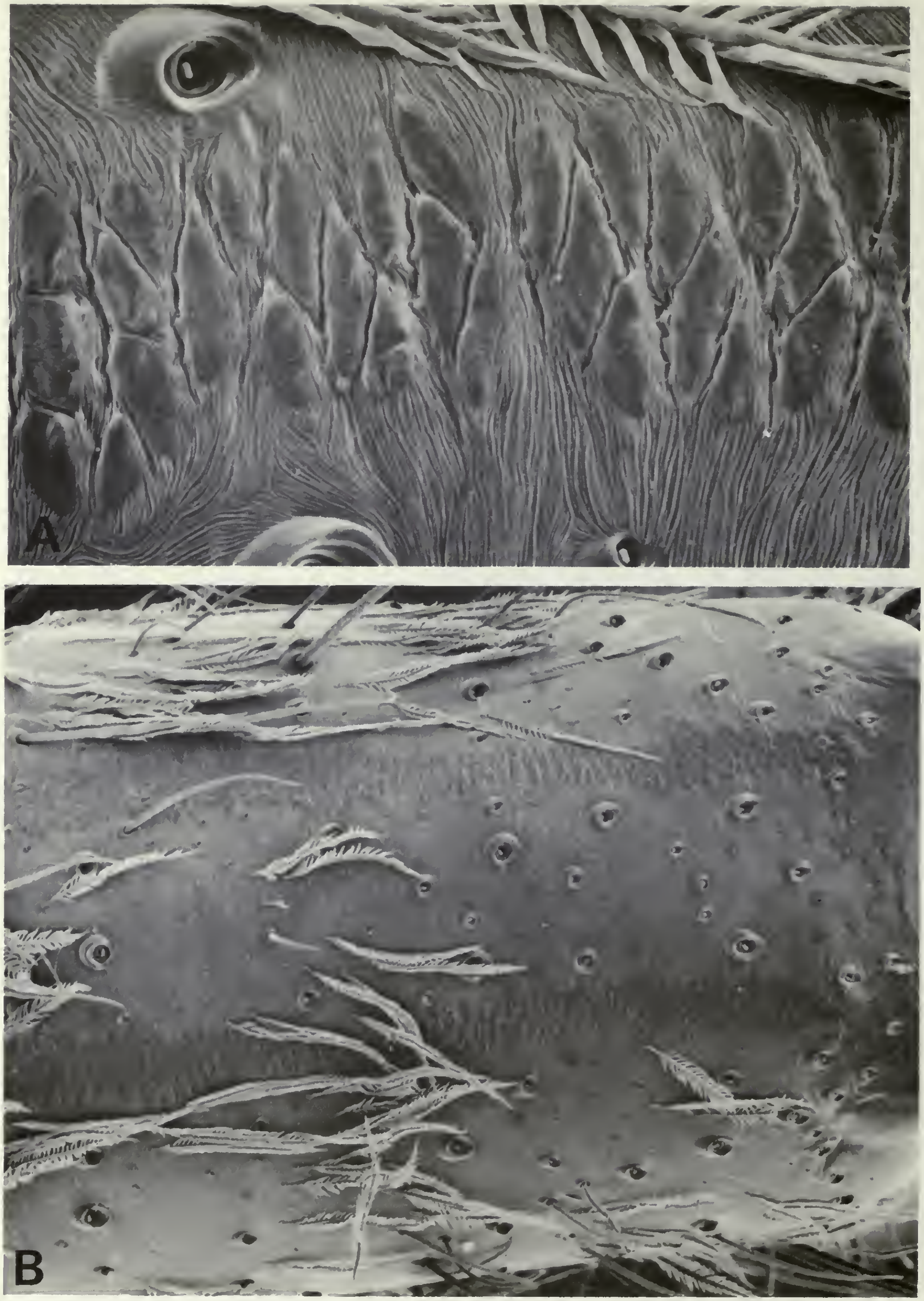

Fig. 15 *Holcolaetis vellerea* Simon, ♀: dorsal surface of tibia I showing hinge lines: A, × 1300; B, × 168.

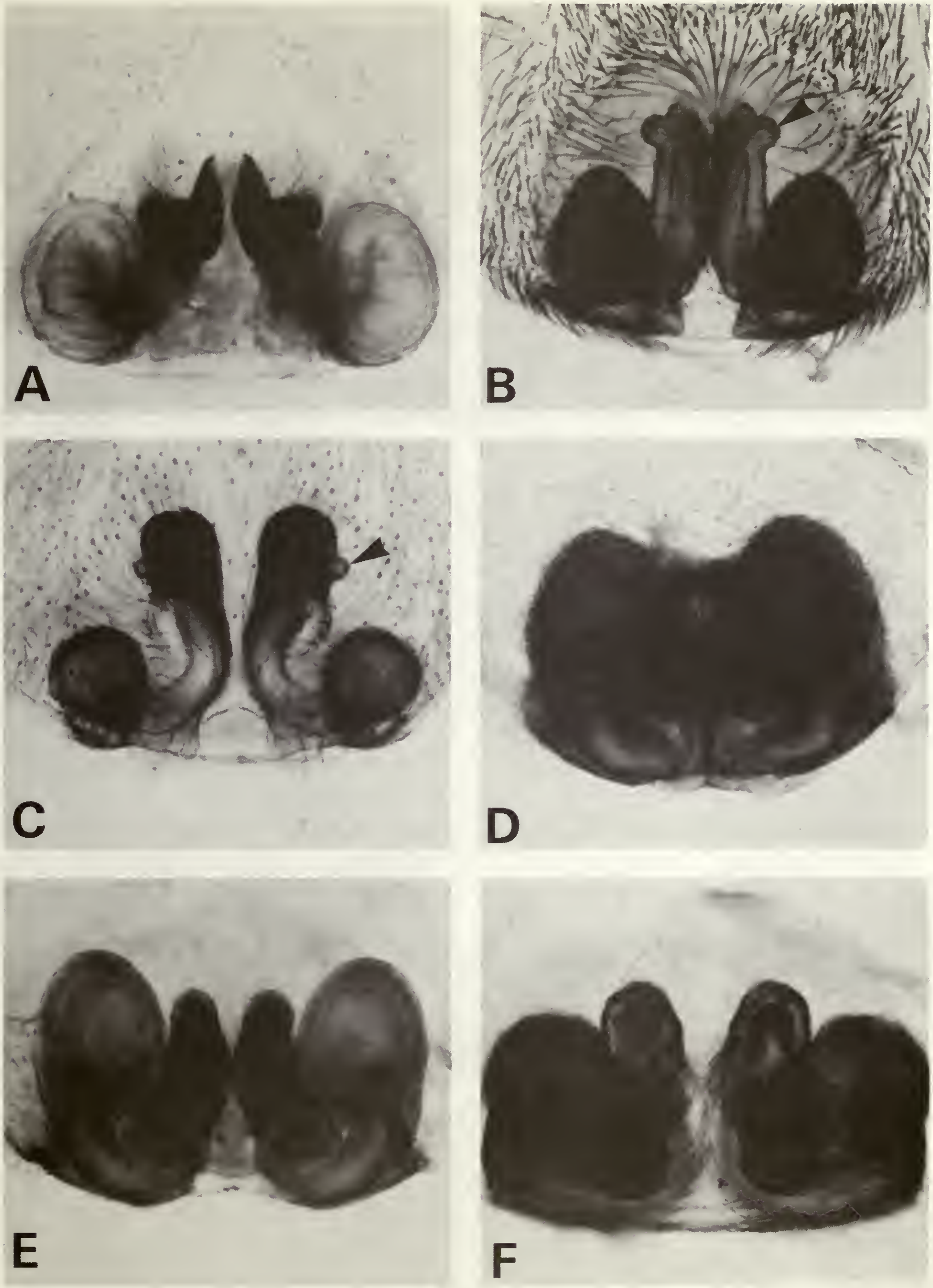

Fig. 16 A, *Holcolaetis xerampelina* Simon, vulva, outer view. B, *H. vellerea* Simon, vulva, outer view; C, *H. zuluensis* Lawrence, vulva, outer view. D, *H. albobarbata* Simon, vulva, outer view. E, *H. clarki* sp. n., vulva, inner view. F, *Sonoita lightfooti* Peckham & Peckham, vulva, inner view.

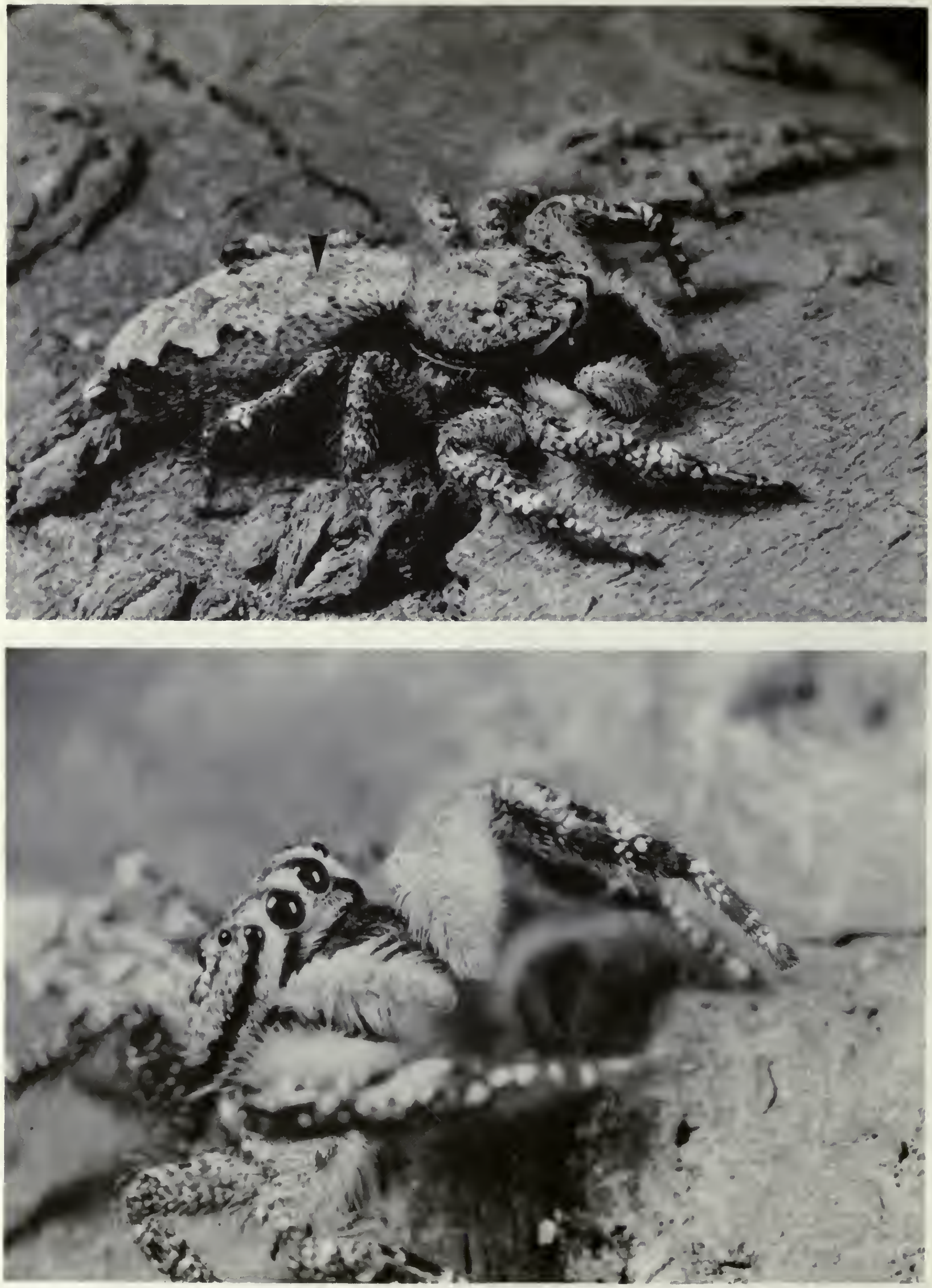

Fig. 17 *Holcolaetis vellerea* Simon, ♀ from Kenya, notice semirecumbent tufts of white hairs on legs and position of pustuliform field indicated, by an arrow.

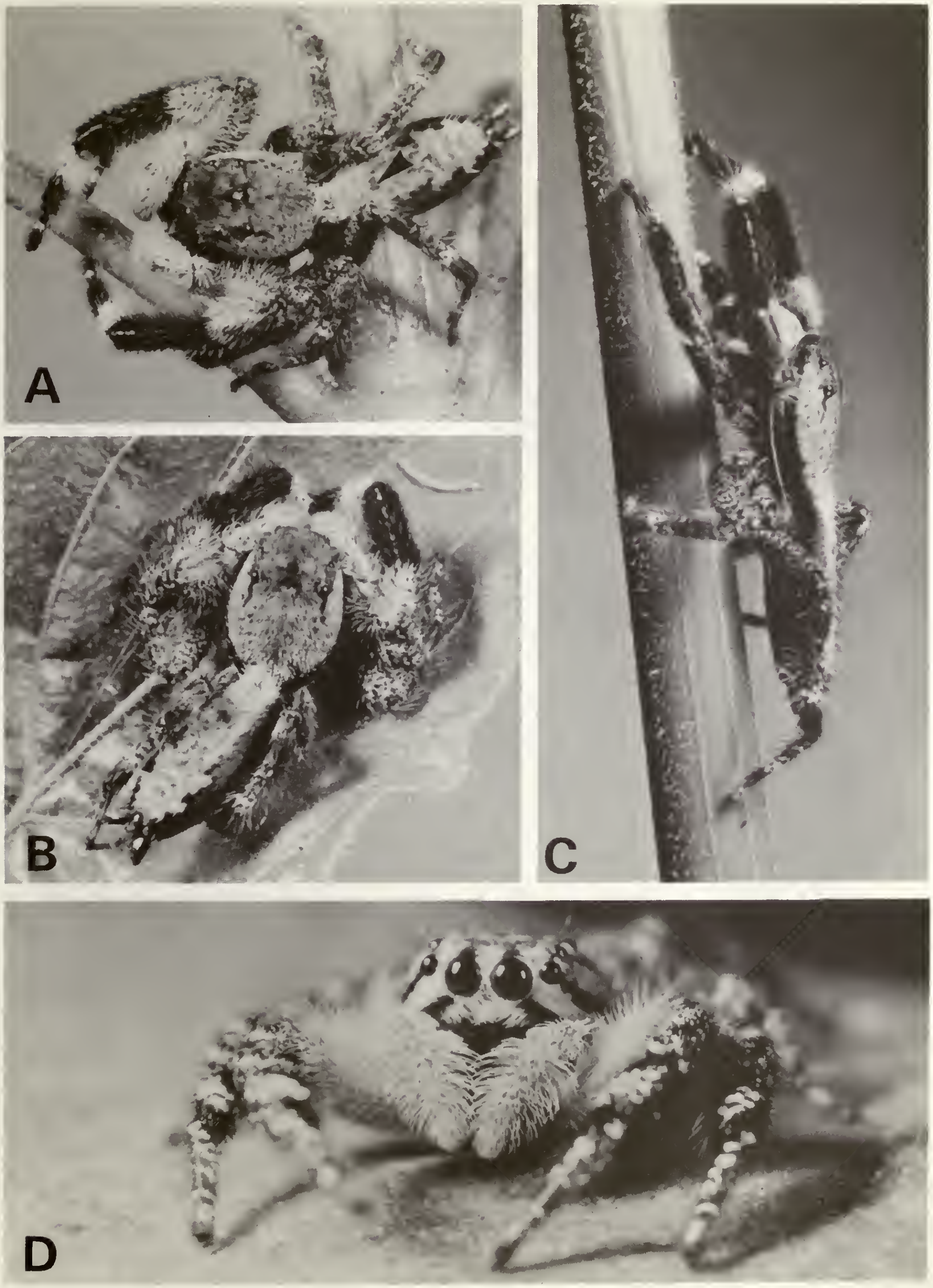

Fig. 18 *Holcolaetis vellerea* Simon, from Kenya: A–C, ♂, pustuliform field indicated by an arrow; D, ♀.

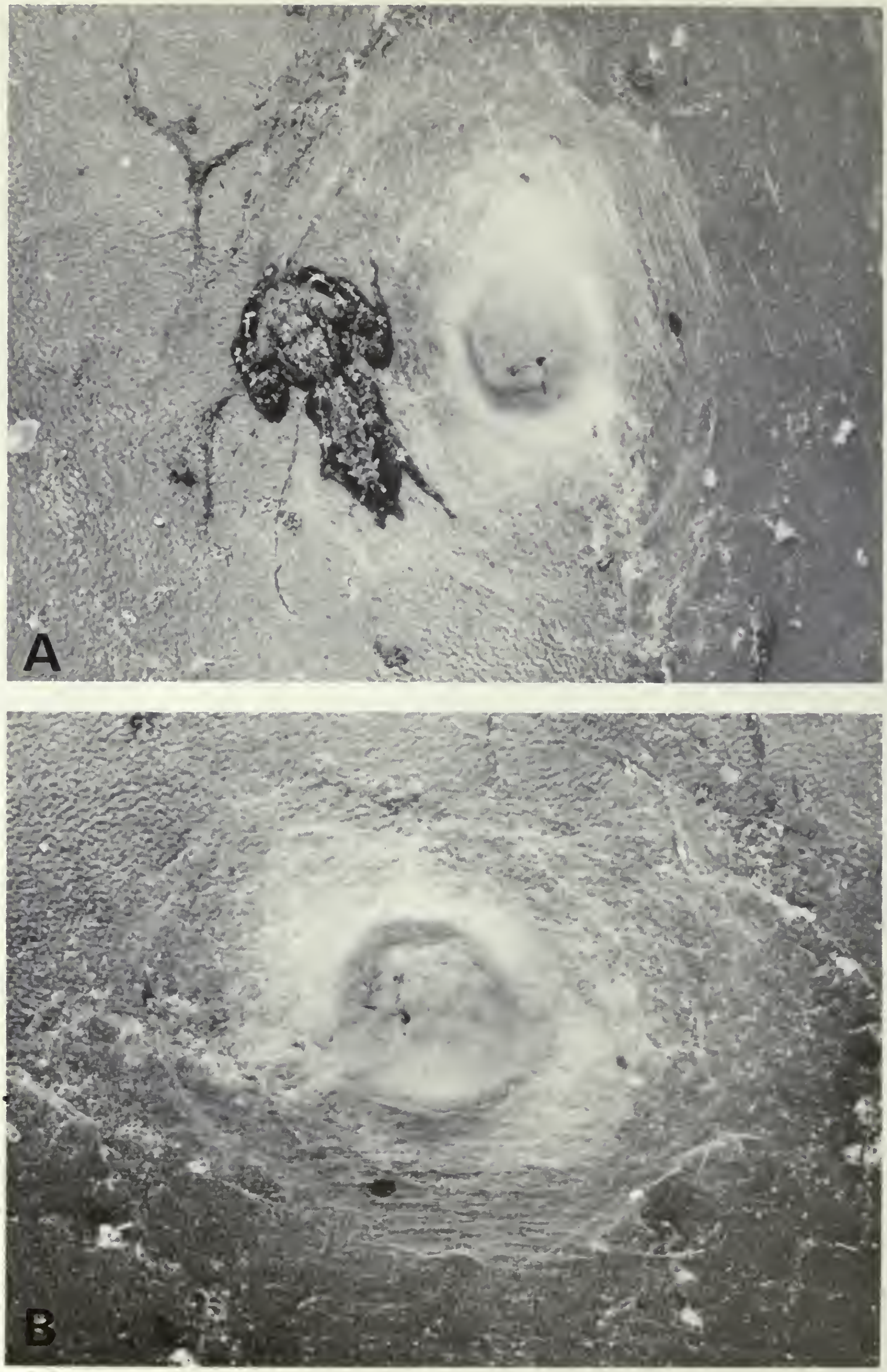

Fig. 19 *Holcolaetis vellerea* Simon, A, ♀ with gnaphosid-like egg-sac; B, egg-sac.

shrinkage in the only available specimens. Provisional observations indicate that the fields are comprised of fewer and more scattered pustuliform organs (Figs 13, 14) and when compared with those of *Holcolaetis,* they are possibly less well developed.

Acknowledgements

I am grateful to Mr & Mrs J. Murphy, London for allowing me to study their important collection of African Salticids. Mrs F. Murphy supplied the photographs for figures 17–18 and Dr R. R. Jackson the photographs for figure 19.

Colleagues kindly made types and other material available for study: Dr R. Jocqué, Musée Royal d'Afrique Centrale, Tervuren, Belgium (MRAC, Tervuren); Dr M. Grasshoff, Forschungsinstitut Senckenberg, Natur-Museum, Senkenberg, Frankfurt am Main, W. Germany (FS, Frankfurt am Main); Dr C. Griswold, Natal Museum, Pietermaritzburg, South Africa (NM, Pietermaritzburg); M. M. Hubert, Muséum National d'Histoire Naturelle, Paris, France (MNHN, Paris); Dr R. R. Jackson, University of Canterbury, Christchurch, New Zealand; Professor T. Kronestedt, Naturhistoriska, Riksmuseet, Stockholm, Sweden (NR, Stockholm); Professor H. W. Levi, Museum of Comparative Zoology, Harvard, U.S.A. (MCZ, Harvard); Ms S. Mascherini, Museo Zoologico de la Specola, Firenze, Italy (MZS, Firenze); Dr N. I. Platnick, American Museum of Natural History, New York, U.S.A. (AMNH, New York).

Finally I would like to thank Mr K. H. Hyatt (BMNH) for reading the manuscript.

References

Bonnet, P. 1957. *Bibliographia Araneorum* **2**(3): 1927–3026. Imprimerie Douladoure, Toulouse.

—— 1958. *Bibliographia Araneorum* **2**(4): 3027–4230. Imprimerie Douladoure, Toulouse.

Brignoli, P. M. 1983. *A catalogue of the Araneae described between 1940 and 1981.* Manchester University Press in association with The British Arachnological Society.

Caporiacco, L. di 1940. Arachnidi raccolti nella regione dei Laghi Etiopici della Fossa Galla. *Atti r. Accad. Ital. Memorie* **11** (18): 767–837.

—— 1941. Arachnida. *Missione Biol. Sagan-Omo.* **12** Zool. 6: 159 pp.

Clark, D. J. 1974. Notes on Simon's types of African Salticidae. *Bull. Br. arachnol. Soc.* **3** (1): 11–27.

Cutler, B. 1976. A catalogue of the jumping spiders of Southern Africa. (Araneae: Lyssomanidae and Salticidae). *Cimbebasia* (A) **4:** 129–135.

Dyal, S. 1935. 4. Spiders of Lahore. *Bull. Dep. Zool. Punjab Univ.* **1:** 119–252.

Humphreys, W. F. 1983. The surface of spiders' eggs. *J. Zool. Lond.* **200:** 303–316.

—— 1985. Spider pheromone 'packets'. *Nature, Lond.* 315 : 104.

Lessert, R. de 1925*a*. Araignées du Sud de l'Afrique. *Revue suisse Zool.* **31** (13): 429–528.

—— 1925*b*. Araignées du Sud de l'Afrique. *Revue suisse Zool.* **32** (21): 323–365.

—— 1927. Araignées du Congo. Part 1. *Revue suisse Zool.* **34** (17): 405–475.

Lawrence, R. F. 1937. A collection of Arachnida from Zululand. *Ann. Natal Mus.* **8** (2): 211–273.

Neave, S. A. 1939. *Nomencl. Zool.* **II,** D–L: 1025 pp. Zoological Society, London.

—— 1940. *Nomencl. Zool.* **IV**, Q–Z, and supplement, 758 pp. Zoological Society, London.

Parry, D. A. 1957. Spider leg-muscles and the autonomy mechanism. *Q. Jl microsc. Sci.* **98:** 331–340.

Peckham, G. W. & Peckham, E. G. 1903. New species of the family Attidae from South Africa, with notes on the distribution of the genera found in the Ethiopian Region. *Trans. Wis. Acad. Sci. Arts Lett.* **14:** 173–278.

Petrunkevitch, A. 1928. Systema Aranearum. *Trans. Conn. Acad. Arts Sci.* **29:** 270 pp.

Prószyński, J. 1971. Catalogue of Salticidae (Aranei) specimens kept in major collections of the world. *Annls zool. Warsz.* **28** (17): 367–519.

Roewer, C. Fr. 1954. *Katalogue der Araneae.* **2,** Abt. B: 924–1290. Institute Royal des Sciences Naturelle de Belgique, Bruxelles.

—— 1965. Die Lyssomanidae und Salticidae—Pluridentati der Äthiopischen Region (Araneae). *Annls Mus. r. Afr. cent.* **139:** 86 pp.

Simon, E. 1886. Études Arachnologiques 18e Memoire (1) XXVI Matériaux pour servir à la faune des arachnides du Sénégal. *Annls Soc. ent Fr.* (6) **5:** 345–396.

—— 1901. *Histoire Naturelle des Araignées* **2** (3): 381–668. Roret: Libraire Encyclopédique, Paris.

—— 1909 (1910). Arachnides recueillis par L. Fea sur la Côte Occidentale d'Afrique 2.e partie. *Mus. civ. Stor. nat. Giacomo Doria* **3** (3): [=44]: 335–449.

Strand, E. 1909. Nordafrikanische, hauptsächlich von Carlo Freiherr von Erlanger gesammelte Oxyopiden und Salticiden (Forts u. Schluss.). *Societas ent.* **23:** 180–181.

Wanless, F. R. 1978. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian Region. *Bull. Br. Mus. nat. Hist.* (Zool.) **33:** 139 pp.

—— 1982. A revision of the spider genus *Cocalodes* with a description of a new related genus (Araneae: Salticidae). *Bull. Br. Mus. nat. Hist.* (Zool.) **42:** 263–298.

—— 1984*a*. A revision of the spider subfamily Spartaeinae nom. n. (Araneae: Salticidae) with descriptions of six new genera. *Bull. Br. Mus. nat. Hist.* (Zool.) **46:** 135–205.

—— 1984*b*. A revision of the spider genus *Cyrba* (Araneae: Salticidae) with the description of a new presumptive pheromone dispersing organ. *Bull. Br. Mus. nat. Hist.* (Zool.) **47:** 445–481.

Waterhouse, C. O. 1902. *Index zoologicus* No I, 421 pp.

—— 1912. *Index zoololgicus* No II, 324 pp.

Manuscript accepted for publication 21 January 1985

Systematics of the New Zealand short-tailed bat *Mystacina* Gray, 1843 (Chiroptera: Mystacinidae)

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Synopsis

Specimens of the short-tailed bat *Mystacina* Gray, 1843 from several localities in New Zealand show that this endemic genus consists of two species. The smaller of these, *M. tuberculata* Gray, 1843, apparently occurs throughout New Zealand, extending to at least some of the associated small islands to the south. The specimens available indicate some intraspecific variation with altitude and latitude and three subspecies are defined, two being described as new. The larger species, *M. robusta* Dwyer, 1962, found until 1965 only on two small southern offshore islands, has not been reported since and is now believed extinct. This species has not been found live on North, South or Stewart Islands since European settlement in the early part of the nineteenth century. The initial description of *M. tuberculata* and other early accounts of this species have been examined in an attempt to establish the original material seen by Gray. The early literature also shows that the other endemic New Zealand bat, *Chalinolobus tuberculatus,* should be ascribed to Gray, 1843 and not to Forster, 1844 as is customary.

Introduction

For many years the unusual endemic New Zealand genus *Mystacina* has been considered to be monospecific, its sole included species *M. tuberculata* Gray, 1843 extending throughout both North and South Islands to the small islands and islets off the extreme southern coast. Although this bat was described nearly 150 years ago, lack of suitable study material has precluded any consideration of variation within the genus until recently. Outside New Zealand it has remained known chiefly from a small number of museum specimens mostly collected during the last century, generally lacking definite locational information, and in some instances damaged. They were sufficiently adequate to establish the features of *Mystacina,* but no more.

Dwyer (1962*a*) reviewed the taxonomic history of the genus and recognised two subspecies of *Mystacina tuberculata* as he then understood it. One, smaller with proportionately longer extremities, occurring in the North Island and at least the northern areas of the South Island, he recognised as *M. t. tuberculata*. For the other, which was larger, with proportionately shorter extremities, and was found on Big South Cape Island off Stewart Island in the extreme south, he proposed the name *M. t. robusta*. Since then, Daniel (1979) and Daniel & Williams (1984) have summarised the distribution of the two supposed subspecies: *M. t. tuberculata* being found to occur on North, South and Little Barrier Islands, *M. t. robusta* found until 1965 only on two islands adjacent to Stewart Island. Daniel (1979) pointed out, however, that both forms were present in several parts of both the North and South Islands until comparatively recently, and that subfossil remains confirmed that this was so within at least the last 3000 years. Interestingly, even as recently as 1962 Dwyer disposed of no more than 11 examples in his examination of the genus. Dwyer (1962*b*) also studied wear on the upper incisors of 12 specimens of *Mystacina* in relation to the length of the skull. These he divided into two groups, one corresponding to *M. t. tuberculata,* the other to *M. t. robusta*. Apart from this, his initial studies were based entirely on external size and features, with no other detailed examination of cranial size and morphology;

Bull. Br. Mus. nat. Hist. (Zool.) **48**(4): 279–300 Issued 31 October 1985

indeed, the skull of the holotype of *M. t. robusta* had to be removed from the specimen in the course of the present work.

More recently, Dwyer (1970) has examined the skulls and limb bones of *Mystacina* from various localities in both North and South Islands and from Stewart Island (see page 298), mostly of subfossil examples from limestone cave deposits. Although he found that specimens from each of the three more northerly latitudes represented by this material fell into two distinct size groups, he considered that in total his measurements did not suggest that two discrete size groups occurred, or that they indicated a north-south separation in size. Instead, he interpreted his results as indicating a continuous range from small to large in each latitudinal sample. This involved accepting a size range for *M. tuberculata* considerably in excess of that found in the majority of bat species of comparable size, but with small individuals lacking from the southernmost samples from Pyramid Valley (North Canterbury), Goulds (Opihi River, South Canterbury), Whitcombe Mountains (Westland) and from Stewart Island. On this basis he rescinded his earlier separation of *M. tuberculata* into two subspecies; nor could he find morphological criteria that would permit separation at the specific level. He remarked that his measurements also suggested that a north-south cline for increasing size might occur, but that size variation was conspicuous for any particular latitude and that the variability decreased from north to south—the latter point a reflection of the absence of small specimens from the southernmost samples. Thus he found that at 30°30′S four skulls ranged from 17·8 to 25·5 mm in length, but at 47°S four others ranged from 23·0 to 23·5 mm in their greatest length. However, the measurements tabulated by Dwyer are largely consistent with the concept of two sympatric species, while Daniel (1979) found that living populations exhibited clear-cut size distinctions in different parts of New Zealand. For this reason Daniel retained the subspecific designations, and further suggested that the marked dimensional differences between the two forms might well justify their recognition as distinct species.

This study is based predominantly on four samples of *Mystacina.* One from Big South Cape Island represents the larger form recognised by Daniel (1979) and includes the holotype of *M. tuberculata robusta* Dwyer, 1962*a*; it is supplemented by a single skeletal specimen from Solomon Island, slightly to the north. The other samples represent the smaller form recognised by Daniel and are from three widely separated localities or areas: Omahuta in the extreme north at 35°10′S, 173°37′E; the upper Waimarino River, Kaimanawa Forest Park, SE. of Lake Taupo, on the volcanic plateau of North Island at 39°02′S, 175°56′E or from localities not far distant; and Codfish Island, off the northeastern coast of Stewart Island at 46°47′S, 167°38′E. The collections of the British Museum (Natural History) have also been available; apart from a few older specimens of indeterminate or uncertain locality these include examples of the smaller form from 'the islands round Stewart Island' and more explicitly from Solomon Island. These obviously were not available to Dwyer (1962*a,* 1970) when he considered the status of *robusta.* Our initial intentions were to establish if possible the relative status of *tuberculata* and *robusta,* and to quantify variation in *Mystacina* so far as we were able to do so. We soon became aware that some doubt existed as to the actual specimens seen by Gray when he initially described the genus and its type species *M. tuberculata,* and, indeed, as to the actual vehicle and date for this publication.

Specimens examined came from the collections of the National Museum (formerly the Dominion Museum), Wellington (DM); the Auckland Institute and Museum (AIM); the Otago Museum, Dunedin (OM); the British Museum (Natural History), London (BM(NH)); and from the collection maintained by M. J. Daniel (MJD). All measurements are in millimetres.

Systematic section

Genus *MYSTACINA* Gray, 1843

Mystacina Gray, 1843*a*: 296. Type species *Mystacina tuberculata* Gray, 1843.

Mystacops Lydekker, 1891: 671. Substitute proposed in the belief that *Mystacina* Gray was preoccupied by *Mystacina* (sic) Boie, 1822, a bird, (Aves), but Boie used *Mystacinus* (Neave, 1940; Dwyer, 1962*a*).

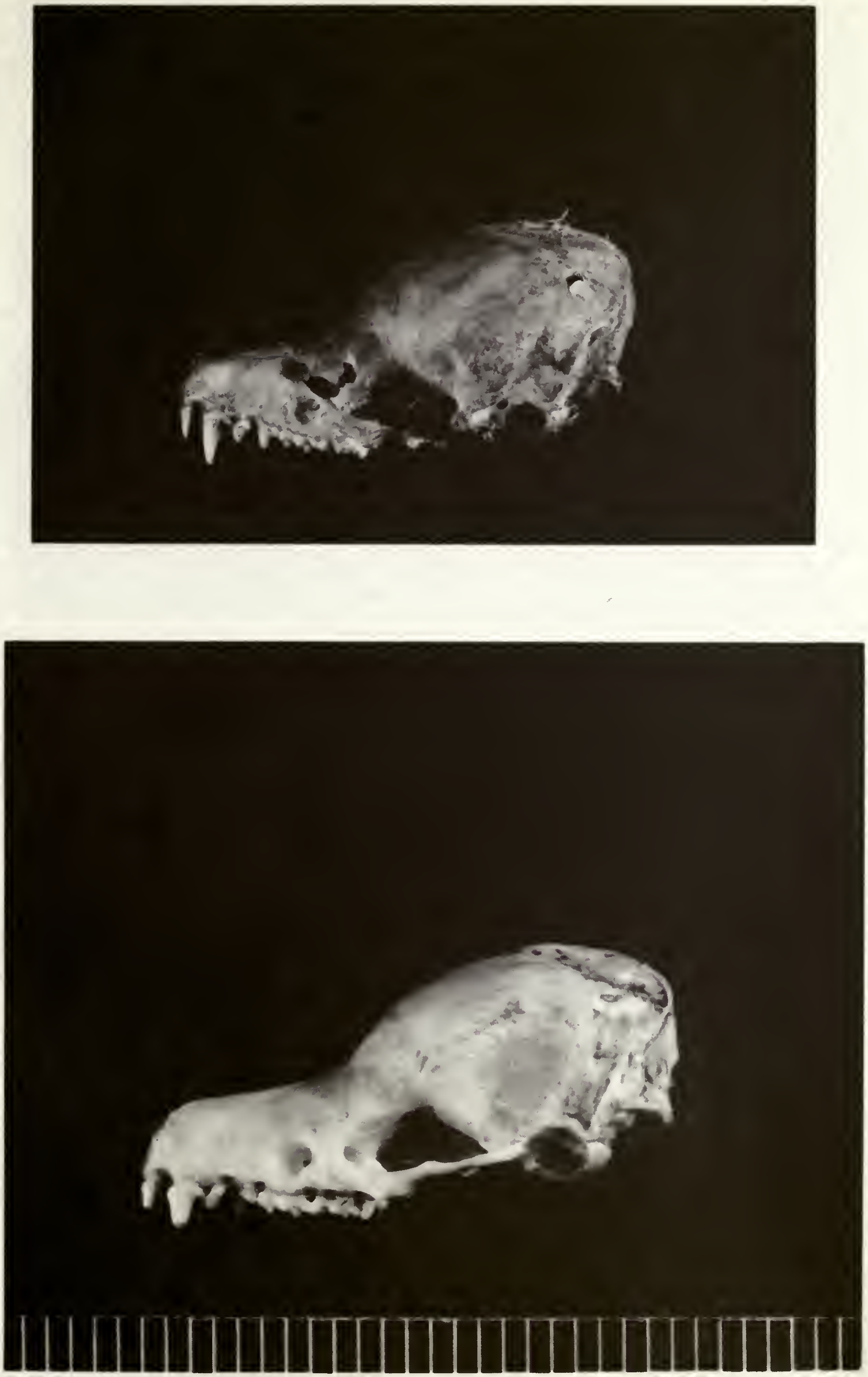

Fig. 1 Lateral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

Dwyer (1962*a*) has provided a precise characterization of the external features of *Mystacina*. The genus may be readily recognized by its conical, obliquely truncated muzzle which has a conspicuous array of stiffened hairs radiating from the posterior margins of its glandular eminences; by its rudimentary narial pad with prominent sublateral narial openings; and by its simple ears and long, simple and attenuate tragus. The limbs are robust, the hindlimbs relatively rather short; the second digit has a single rudimentary phalanx, the third digit three bony phalanges and a cartilaginous tip, its first phalanx flexed above the metacarpal when at rest; the fifth digit is much longer than the metacarpal of the third digit, its cartilaginous tip extending slightly beyond the edge of the wing membrane. The flight membranes are thick and leathery, the propatagium reduced, the wing inserted at the ankle, with the upper surface of the plagiopatagium and the uropatagium extensively ridged near the body; the uropatagium is narrow, the short tail projecting from its upper surface.

The skull (Figs 1–7) has an elongate, rounded braincase and strong, tubular rostrum; the narial emargination is broad and deep, rounded and almost tubular; the palatal branches of the premaxillaries enclose two lateral anterior palatal foramina; the zygomata are slender, narrow and short, almost uniformly convexly curved in dorsal aspect; the anteorbital foramen is separated by a broad bar of bone, its anterior and posterior openings large, the latter occupying most of the anterior orbital wall; palate narrow anteriorly, wide posteriorly, the maxillary toothrows strongly convergent; there is a short bony post-palatal extension with U-shaped palation and the palate as a whole is slightly domed; the pterygoids are more or less parallel, the foramen rotundum large, coalesced with the optic foramen, the resulting aperture at its widest anteriorly where it is squarely truncate in outline; the audital bullae are large and well developed, their inner face unemarginated, the tympanic bullae very large, almost completely enclosing the cochleae: the basioccipital is broad, nearly as wide as one auditory bulla.

Eight palatal ridges, the anterior six undivided, the first lying between the canines, the second flexed slightly forward between the anterior premolars (pm^{2-2}); third more strongly curved forward between antero-internal corners of the second premolars (pm^{4-4}); fourth similarly curved between antero-internal corners of m^{1-1}; fifth slightly less strongly curved, joining the interspaces between m^1 and m^2; sixth straight, joining centres of internal faces of m^{2-2}; seventh and eighth shallowly divided medianly, strongly flexed, especially towards the centre of the palate, seventh originating at the interspace between m^2 and m^3, the eighth originating from the centre of the inner faces of m^{3-3}.

Dental formula i 1/1, c 1/1, pm 2/2, m 3/3 = 28. The upper incisors are large, with oblique crowns, separated basally, but in contact at about one half their height, their tips divergent, each tooth anteriorly convex, posteriorly concave, with slight lateral and posterior basal cusps; the upper canines are well developed, separated from the incisors by a narrow interspace; the upper premolars (pm^2, pm^4) are large, with pm^2 slightly the smaller, its base more or less triangular, pm^4 with distinct antero-internal cusp, the base of the tooth subsquare, both pm^2 and pm^4 with a rounded postero-internal basal cusp; the upper molars are normal, m^1 and m^2 with a long, low protocone, its commissure flexed abruptly downwards posteriorly, the inner margins of the teeth squarely truncate, each with a narrow postero-internal heel, more obviously developed in m^1; m^3 with large metacone and third commissure. The lower incisors are small but functional, compressed between the canines, deeply tricuspid and strongly expanded posteriorly, their longitudinal diameter greater than their transverse diameter; the lower canines are massive at the base and are narrowly separated posteriorly, their antero-internal margins with a distinct notch into which the outer cusp of the incisor fits; the lower premolars (pm_2, pm_4) are similar in size, pm_2 very slightly narrower than pm_4; lower molars with no especial peculiarities, m_3 with distinct entoconid and hypoconid.

The genus is endemic to New Zealand. Its two included species may be keyed:

Smaller, length of forearm 40·0–45·0 mm, condylobasal length 17·3–19·1 mm, canine to third molar (c–m^3) 7·3–8·0 mm, ears relatively long, extending to or beyond tip of muzzle when laid forward . . . . **M. tuberculata**

Larger, length of forearm 45·3–47·5 mm, condylobasal length 21·0–22·5 mm, canine to third molar (c–m^3) 8·9–9·4 mm, ears relatively shorter, not reaching to tip of muzzle when laid forward . . **M. robusta**

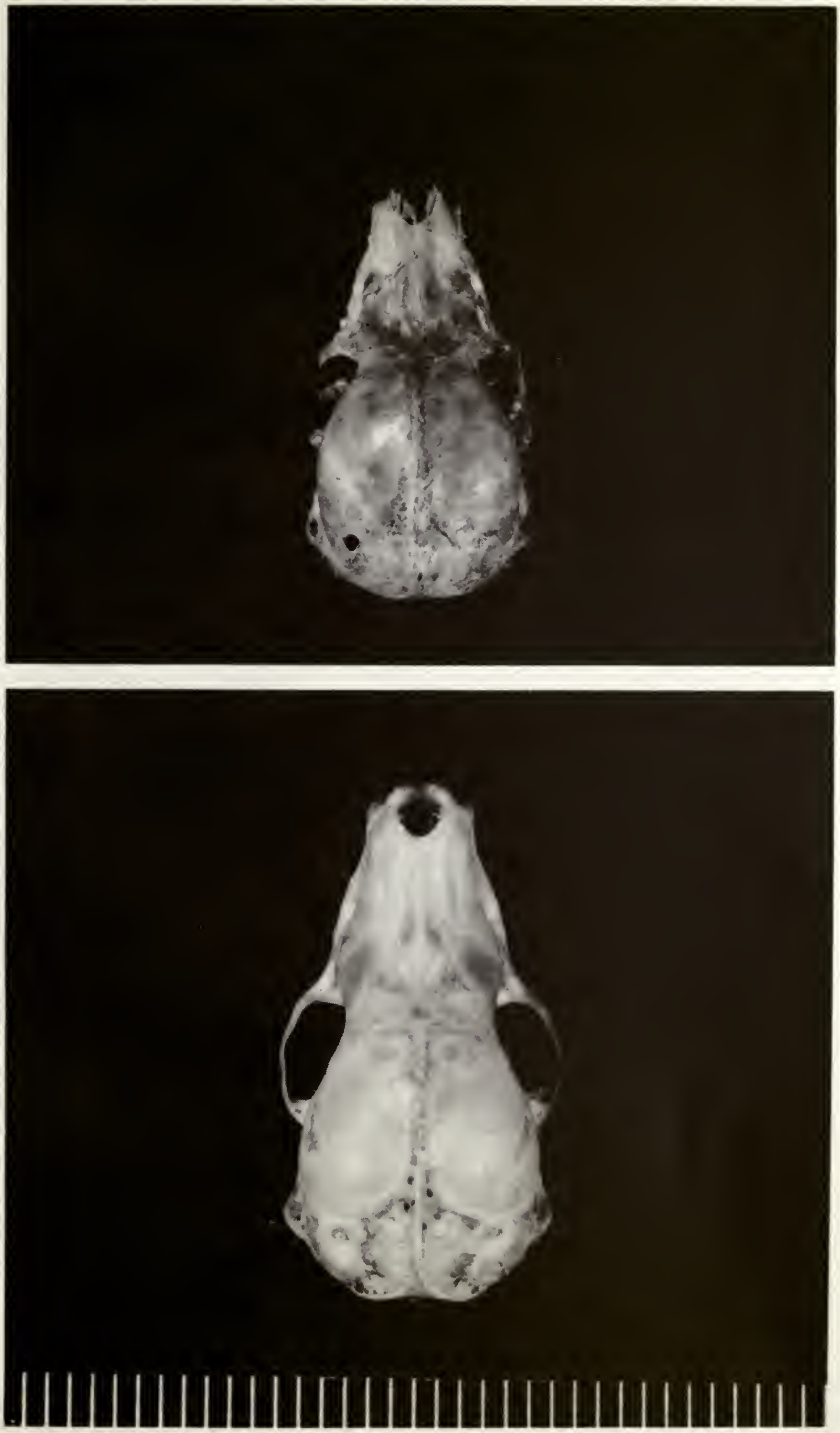

Fig. 2 Dorsal view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

Mystacina tuberculata Gray, 1843

Mystacina tuberculata Gray, 1843*a*: 296. 'New Zealand'.

Mystacina velutina Hutton, 1871: 185. Substitute: proposed to avoid the two species of bat known to be native to New Zealand sharing the same specific epithet.

ORIGINAL DESCRIPTION. The original account of *Mystacina tuberculata* has been variously cited. Tomes (1857), who may be properly regarded as first reviser, gave as its initial reference Gray's *List of the specimens of Mammalia in the collections of the British Museum,* p. 34, 1843. He added 'Gray in Dieffenb. Journ. App. p. 296, 1843'; 'Gray, Zool. Voy. Sulphur. No. II, p. 23, 1843' and 'Zool. Voy. Erebus and Terror, No. IV, pl. 22, 1844'. The names *Mystacina* and *Mystacina tuberculata* have since been attributed to one or another of these sources.

Dieffenbach, E. *Travels in New Zealand: with contributions to the geography, geology, botany and natural history of that country.* Both volumes are dated 1843; according to Sherborn (1922: xliv, cxxxiv) this work was published in January of that year. Gray (vol. 2, p. 296) properly diagnoses and describes *Mystacina tuberculata,* but in the belief that this was the bat illustrated and described, but not then published, by Forster.

Gray, J. E. *List of the specimens of Mammalia in the collections of the British Museum.* This work is dated 1843: Gray has suffixed his introductory remarks 'May-Day, 1843', and it must be presumed that it appeared after that date. Moreover the mention of *Mystacina tuberculata* (p. 34) lacks descriptive matter and the name is thus a nomen nudum in this instance.

Gray, J. E. *The Zoology of the Voyage of H.M.S. Sulphur under the command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S., etc.* This book is clearly dated 1844 and this date is attributed to it in the Catalogue of the Library of the British Museum (Natural History). Its erroneous dating of 1843 by some authors (i.e. Dobson, 1878; Honacki *et al.,* 1982) appears to be through confusion with the actual narrative of the voyage by Belcher, in two volumes (Belcher, E., *Narrative of a voyage round the world, performed in H.M.S. Sulphur, during ... 1836–1842, etc.*) which is dated 1843 but which contains no mention of *Mystacina.* Moreover this account shows that H.M.S. *Sulphur* did not visit New Zealand.

Gray, J. E. *The Zoology of the Voyage of H.M.S. Erebus & Terror under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839–1843.* This work evidently appeared in a number of parts. The section on Mammalia by J. E. Gray consists of three separate articles each clearly dated on the title page, the work as a whole being dated 1844–1875. The three parts on Mammalia are: *I. The seals of the Southern Hemisphere* (pp. 1–8), 1844, (pp. 9–12), 1875; *II. Miscellanea,* (pp. 12a–12d), 1875; and *III. On the Cetaceous Animals* (pp. 13–53), 1846. The account of *Mystacina tuberculata* appears in the *Miscellanea,* p. 12b. No dates are given for the plates. The British Museum (Natural History) copy of this work has a manuscript note on the first page of the *Miscellanea* article which reads 'Plates prepared in 1845, & seen privately by Krefft and other quoters, but only published, with the text, in 1875'.

It is clear, therefore, that *Mystacina* and *Mystacina tuberculata* must be cited from Gray, 1843, *in* Dieffenbach, vol. 2, p. 296, as Thomas (1905) recognized when accepting this work as the prior account, although rejecting *Mystacina tuberculata* Gray, 1843 in favour of *Mystacops velutinus* (Hutton, 1871) on other grounds.

THE TWO NATIVE NEW ZEALAND BATS. There has in the past been nomenclatorial confusion between the two native species of bat known to inhabit New Zealand, namely *Mystacina tuberculata* Gray, 1843, and *Chalinolobus tuberculatus,* usually attributed to Forster, 1844. This confusion stems from Gray, who believed the specimens that he described in 1843 (*in* Dieffenbach, p. 296) in fact represented the species seen and illustrated by Forster many years before, but whose illustration was not published until 1844. In fact, Gray on an earlier page of Dieffenbach's Travels (vol. 2, p. 181) applied the name *Vespertilio tuberculatus* to Forster's then unpublished material. The matter was resolved by Tomes (1857) who for the first time formally recognised that two species were involved, which he called *Scotophilus tuberculatus* Forster, 1844 (= *Chalinolobus tuberculatus*), and *Mystacina tuberculata* Gray, 1843. These are essentially the usages of the present day.

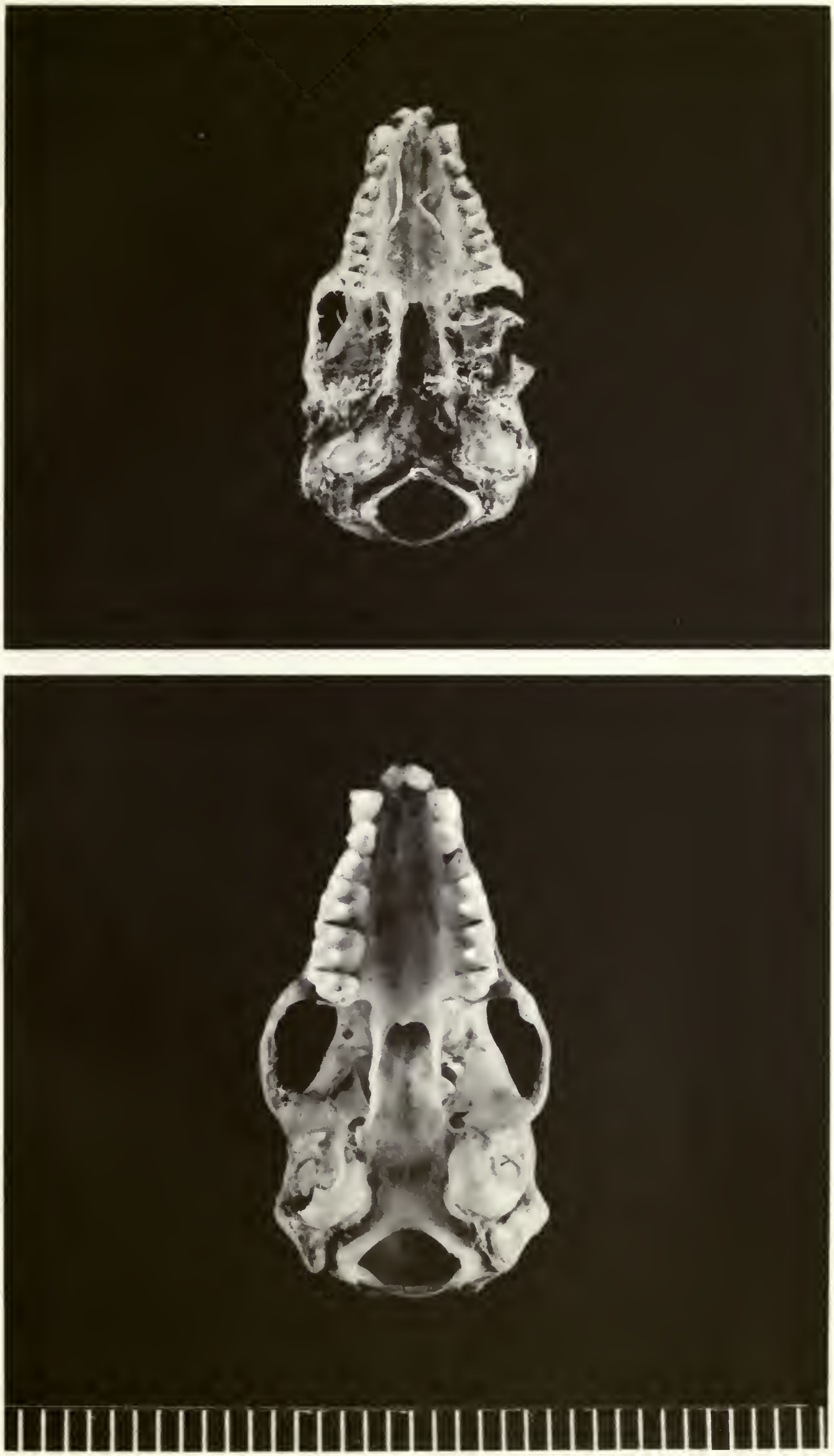

Fig. 3 Ventral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

The first usage of *Vespertilio tuberculatus,* however, is not by Forster in 1844, but by Gray on p. 181 of volume 2 of Dieffenbach's Travels, wherein Gray provides a list of the Mammalia hitherto recorded as found in New Zealand. Under the heading Vespertilionidae he gives the entry:

1. *Vespertilio tuberculatus.* G. Forster. Icon. ined., n. 1.
Yellowish brown; ears small, rounded.
Inhab. Dusky Bay, New Zealand. G. Forster.

He remarks: 'I am not aware that any of these animals [i.e. bats] have reached Europe; they would be interesting, and doubtless new.' He also records Dieffenbach's opinion that in New Zealand . . . 'There is, apparently, only one species; probably the one figured by Forster.' Thus *Vespertilio tuberculatus* Gray, 1843 is based on the then unpublished drawing by Forster, which did not appear until the following year. As Thomas (1905) pointed out, Gray's usage of the name must take precedence and the name *Chalinolobus tuberculatus* must be ascribed to Gray, 1843, *in* Dieffenbach, vol. 2, p. 181.

Subsequently Gray, *in* Dieffenbach, vol. 2, p. 296 under the heading *'Vespertilio tuberculatus,* p. 181', stated that he had just received two specimens of this bat which he recognised as a new genus. He provided a brief description and says 'It may be called *Mystacina tuberculata'.* Thus, although under the impression that this was the bat first discovered by Forster, Gray provided the initial account of the short-tailed bat. This situation was first discussed by Thomas (1905), who recognised that the five words of description by Gray on p. 181 of Dieffenbach's second volume were sufficient to establish *Vespertilio tuberculatus* in the authorship of Gray. Thomas, however, considered that Gray's later use of *tuberculata* in combination with *Mystacina* on p. 296 of the same work (in the belief that his newly obtained specimens represented the same species) was invalidated by his previous action. As a result, Thomas employed the substitute name *velutina,* first proposed by Hutton (1871) to avoid the two native New Zealand bats sharing the same specific name. This concept has not gained general acceptance and the short-tailed bat has been known for many years as *Mystacina tuberculata.* Moreover, the International Code of Zoological Nomenclature appears to provide no support for Thomas' contention. The taxonomic history of *Mystacina* and its substitute *Mystacops* is summarized by Dwyer (1962*a*).

ORIGINAL MATERIAL. Gray stated (1843*a*: 296) that he had received two specimens of *Mystacina tuberculata,* and in his List of Mammalia in the collections of the British Museum (1843*b*: 34) he specifies two examples 'a' and 'b'. Dobson (1878), in listing the holdings of the British Museum at that date, records four specimens that apparently originate from the decade 1840–1849:

a.	ad. sk.	(type)	New Zealand.	
		(Figured in the 'Voyage of the Erebus and Terror.')		
b.	ad. sk.		New Zealand	Sir E. Belcher
c.	ad. sk.		New Zealand	Sir G. Grey [C.]
g.	skeleton	(imperfect)		

Oldfield Thomas has annotated specimen 'a' in a copy of Dobson's Catalogue in the library of the British Museum (Natural History) with the superscription 'Dr. F. J. Knox (P.)—see Trans. N.Z. Inst. IV, p. 186, 1871' and has added 'F. J. Knox (P.)' to specimen 'g'. Nothing can now found of any specimen from Belcher and there is no example of *Mystacina* recorded in the accession registers under this donor.

The remaining specimens listed by Dobson can be shown to be of a later date. They are:

d.	♀ ad., al.	New Zealand	Capt. Stokes [P.]
e,f.	ad. sks., in al.	Wellington, New Zealand	Colonial Museum [P.].

The specimen from Captain Stokes is one of three accessed in 1853 (BM(NH) 53.2.14.1–3) but none can now be found. Those from the Colonial (= National) Museum, Wellington, date apparently from 1876 but the accession register records that only a single specimen (BM(NH) 76.4.8.1) was formally entered into the collections.

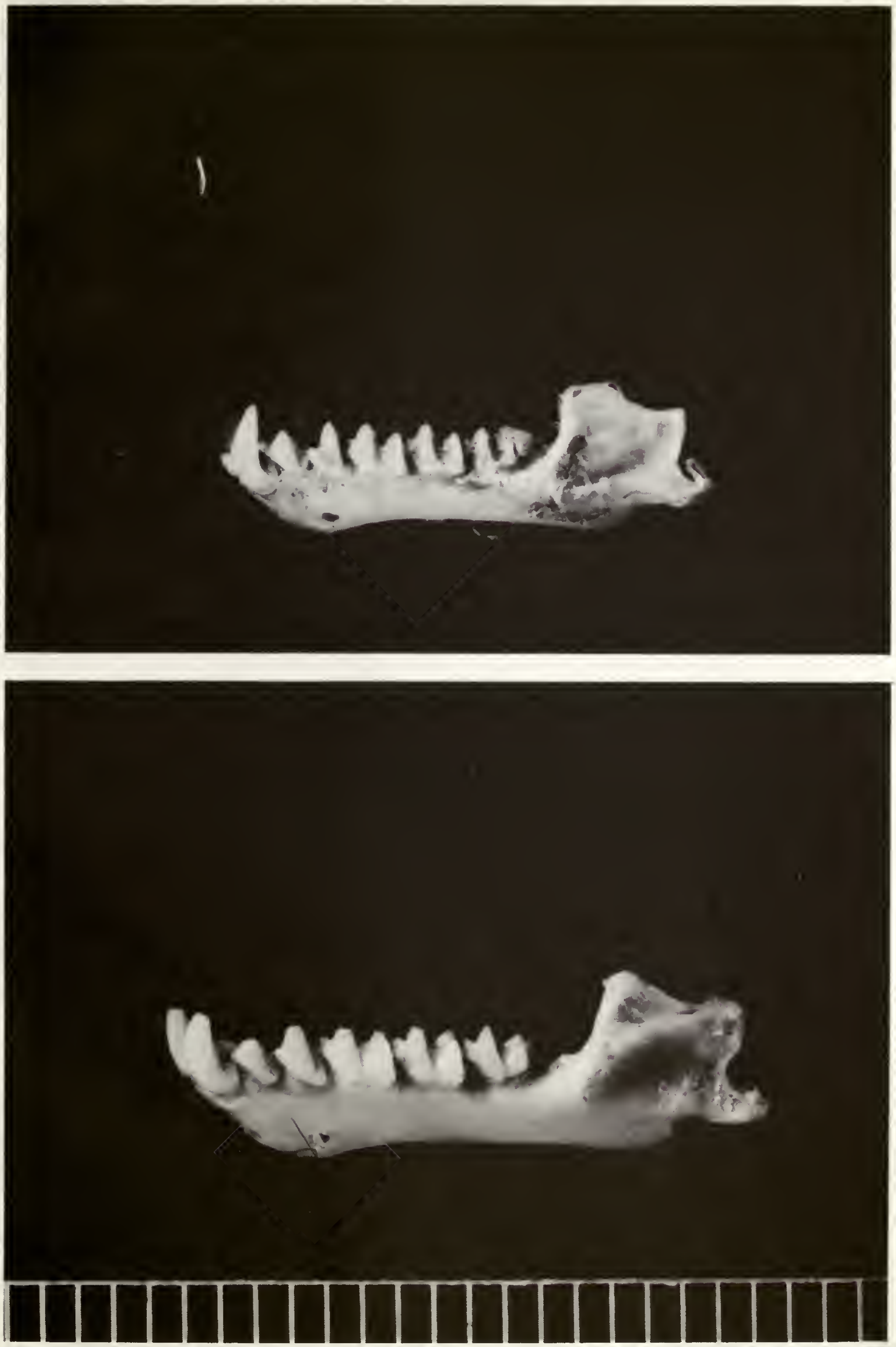

Fig. 4 Lateral view of mandibles: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

There are now four specimens of *Mystacina* from the decade 1840–1849 in the collections in London, with a further example that may date from this period. They are:

> BM(NH) 42.2.8.10. New Zealand. Sir G. Grey. This is specimen 'c' of Dobson and is so marked. It is now a skin and skull but may at one time have been a mounted example. No trace of this accession number can be found in the appropriate register.
>
> BM(NH) 44.10.29.7. New Zealand. This adult skin and skull, which likewise has evidently once been a mounted specimen, bears a label in the hand of R. F. Tomes 'Fm. Brit. Mus. Coll. Feb. 1857. Lab. 44.10.29.7. Skull fig. by Ford. 117B'. The skin also has a more modern label that carries no indication of the origin of the specimen, but a similarly more modern label on the skull indicates that the specimen came from Dr Knox. The accession register has entries 44.10.29.6 and 44.10.29.7 but these are bracketed together and are suffixed 'No. 7'. According to the register this material was presented by Dr Fred Knox of Port Nicholson, New Zealand. The more modern label on the skin notes that the specimen returned to the British Museum in the Tomes Collection in 1905.
>
> BM(NH) 44.10.29.16. Part skeleton. This is specimen 'g' of Dobson. The register entry shows this also to have come from Knox and is cross referenced 'see 44.10.29.6' and 'Stuffed specimen in Coll^{n}'. Knox (1871) stated that in July, 1843 he had sent the skeleton, skin and other parts of an example of *Mystacina* to the British Museum and the inference must be that 44.10.29.6–7 and 44.10.29.16 are the accession numbers of this material.
>
> BM(NH) 49.3.2.1. New Zealand. Sir G. Grey. A skin and skull, marked 'c*' and so added in manuscript to Dobson's Catalogue by Thomas.
>
> BM(NH) 7.1.1.623. This young adult skin and skull, which again shows signs of having once been mounted, is from the Tomes Collection, received at the British Museum in 1905. The skin has been labelled by R. F. Tomes 'Fm. British Museum Jan. 1856. New Zealand. 117a'. More recent additions give the accession number and record its onetime presence in the Tomes Collection, the skull having similar more modern labels. Obviously this specimen was in the British Museum before 1856, but beyond this nothing certain can be established of its history. The register entry 44.10.29.6 carries the annotation 'Specimen with Mr Tomes 1856', perhaps suggesting that Knox might have sent two examples, one given to Tomes by Gray in 1856, the other, 44.10.29.7, given to him in 1857. However, it is now impossible to determine whether the entries 44.10.29.6–7 and 44.10.29.16 all refer to parts of a single specimen or to two specimens. Both 44.10.29.7 and 7.1.1.623 appear to have remained in the Tomes Collection for almost 50 years, and if specimen 'a' of Dobson is in fact 44.10.29.7 from Knox as Thomas thought it was, then Dobson must have recorded it while it was absent from the collections of the British Museum.

It is also interesting that the accession records of the collection presented by Dr Knox (BM(NH) 44.10.29.6–16) include a fourth entry for a bat, 44.10.29.8, which Gray has recorded as *Vespertilio tuberculata*, in contrast to the other three entries (44.10.29.6–7, 44.10.29.16) for which he has used *Mystacina tuberculata*. The specimen is still in the collections and is an example of *Chalinolobus tuberculatus* (Gray, 1843). This shows that when the register entry was completed by Gray, presumably in the latter part of 1844, he had by then distinguished the two native New Zealand bats one from the other, although initially he had believed the specimens that he called *Mystacina tuberculata* to represent the species illustrated by Forster but not then published. BM(NH) 44.10.29.8 appears to be specimen 'i' of Dobson (1878: 249), who considered it to be that figured and described by Gray in the *Voyage of the Erebus and Terror*, 1875. Thomas has annotated a copy of Dobson in the library of the British Museum (Natural History) to the effect that specimen 'i' is from New Zealand and from Dr Knox; Dobson has labelled it as the original of the figure and description by Gray in 1875. Thus Dr Knox was most probably the first to provide specimens of both native New Zealand bats in the same collection, perhaps as early as 1843, although it was not until Tomes (1857) published his detailed study of both species that their co-existence in New Zealand was formally recognized.

Gray did not designate a holotype for *Mystacina tuberculata*, and although it is evident that his two syntypes were at one time in the collections of the British Museum (probably 'a' and 'b' of his

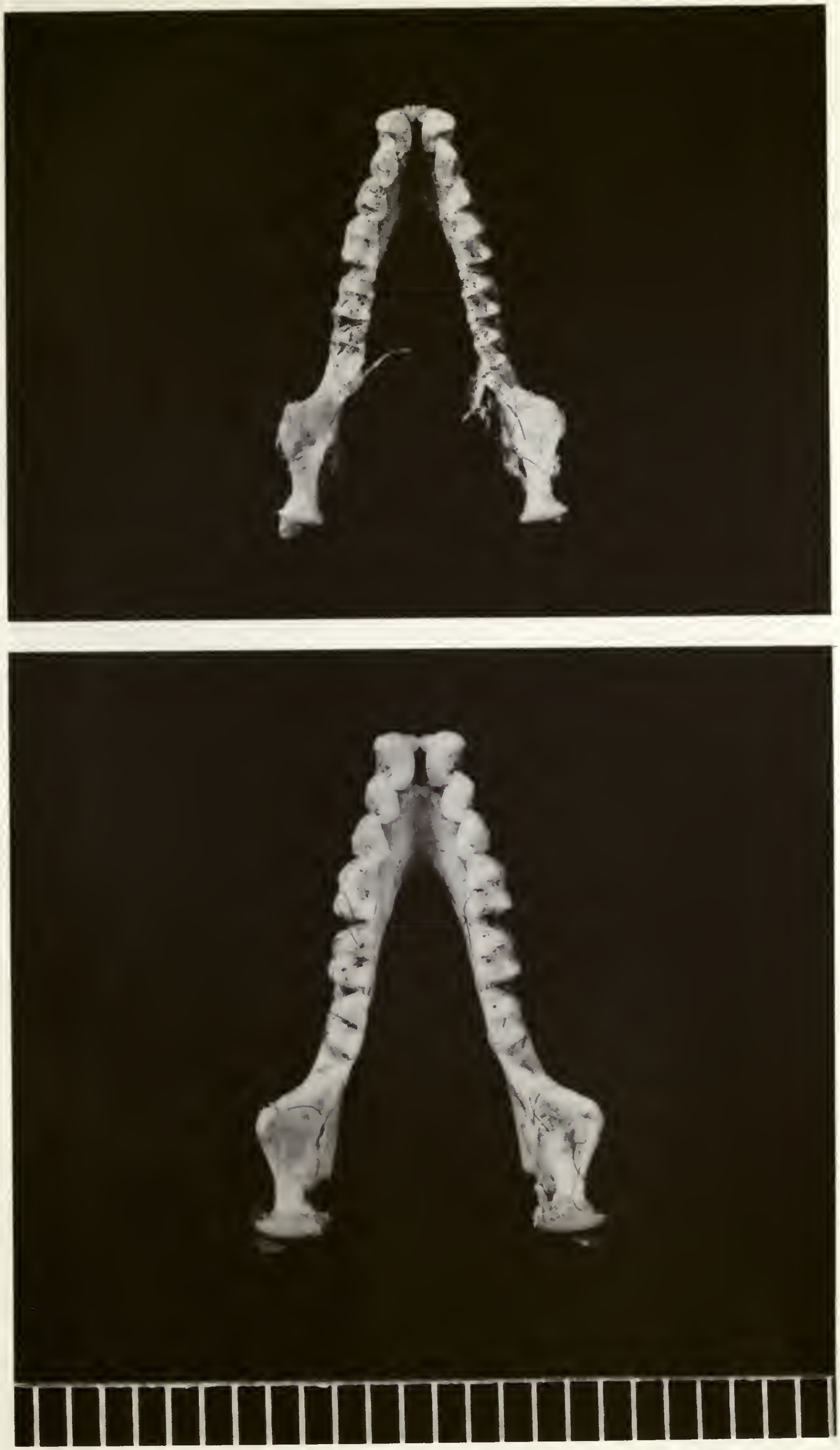

Fig. 5 Dorsal view of mandibles: (above) *Mystacina tuberculata tuberculata* BM(NH) 44.10.29.7, 'New Zealand'; (below) *Mystacina robusta* Holotype DM 1083, Big South Cape Island.

List of Mammalia, etc., 1843) there now seems no possibility of identifying either with certainty. It is even possible that they have been destroyed or have passed out of the Museum collections. Gray did provide Tomes, for instance, with the 'necessary materials' for his revision (1857), which Tomes gratefully acknowledged, at the same time keeping the specimens in his own collection. Since it is necessary to settle *tuberculata* on one or other of the two species now recognised in New Zealand, and since neither the survival nor the destruction of the syntypes can be proved, we propose that the species be interpreted by reference to one or other of the specimens from this period now in the British Museum (Natural History). Three possible candidates can be considered. Of these, BM(NH) 42.2.8.50 from Sir George Grey is young, and this collector and donor is nowhere mentioned by Gray in any of his accounts of *Mystacina tuberculata*. BM(NH) 7.1.1.623 from the Tomes Collection cannot be traced with certainty beyond 1856, and is also a young adult. The obvious choice is then BM(NH) 44.10.29.7, apparently the specimen that Dobson (1878) considered the type. This skin and skull, which was presented by Dr F. J. Knox and is therefore possibly from the environs of Port Nicholson (= Wellington), is accordingly that on which we base our interpretation of *Mystacina tuberculata* Gray, 1843. The skull is figured by Tomes (1857); if the identity with specimen 'a' of Dobson (1878) is correct, then the skin is probably the original of the plate by Gray in the *Zoology of the Voyage of the Erebus and Terror*, 1875.

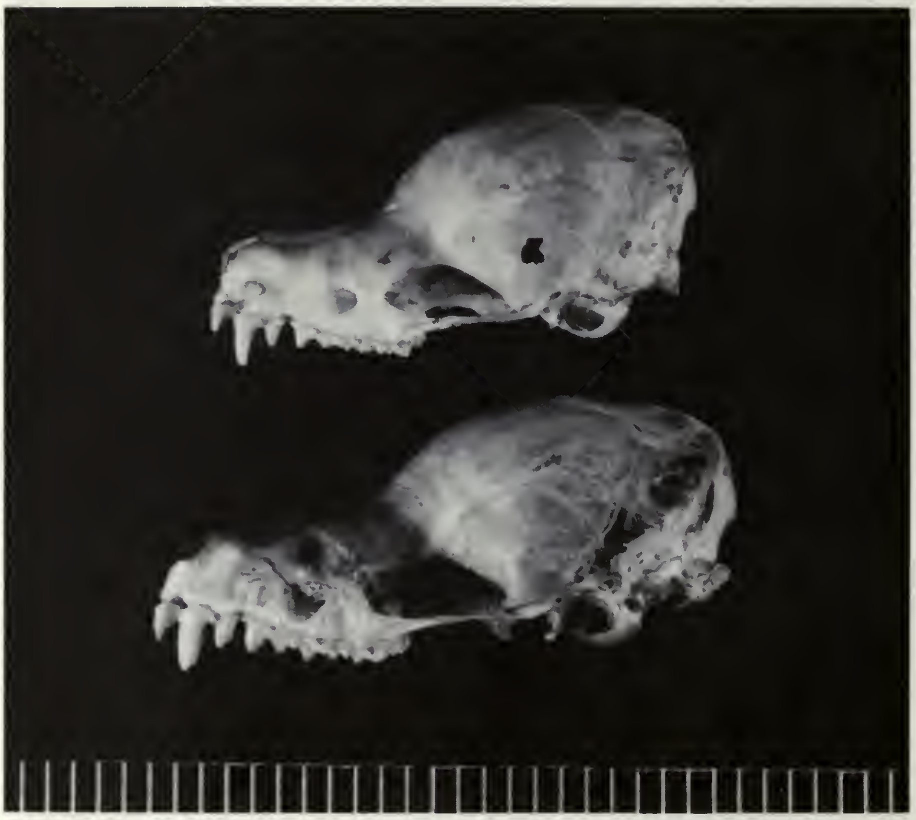

Fig. 6 Lateral view of skulls: (above) *Mystacina tuberculata tuberculata* BM(NH) 62.2116; (below) *Mystacina robusta* DM 1554, both from Solomon Island, off Stewart Island.

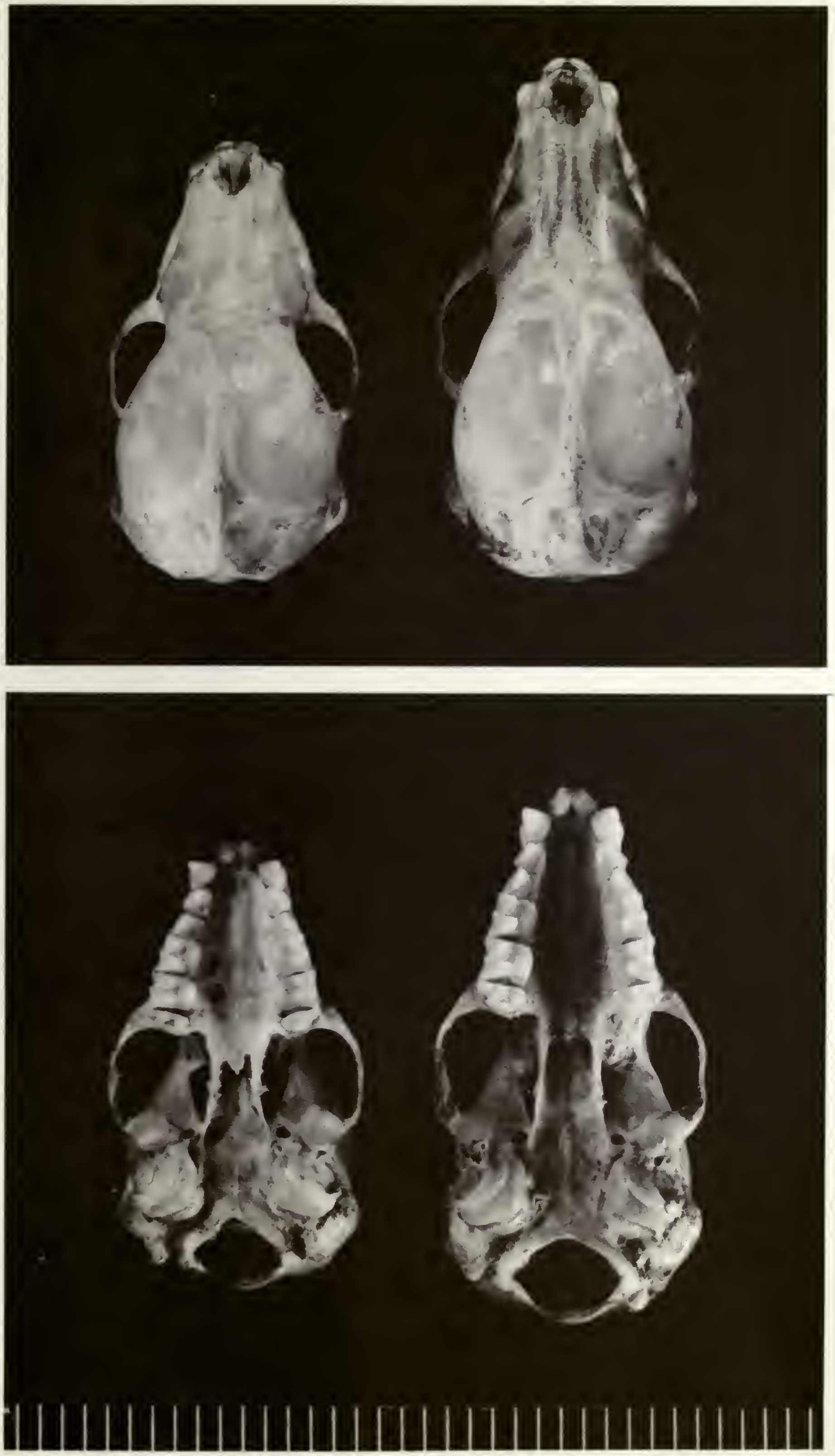

Fig. 7 Dorsal (above) and ventral (below) view of skulls: (left) *Mystacina tuberculata tuberculata* BM(NH) 62.2116; (right) *Mystacina robusta* DM 1554, both from Solomon Island, off Stewart Island.

Table 1 External measurements of *Mystacina tuberculata* and *M. robusta*.

		M. tuberculata									*M. robusta*	
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'	*M. t. tuberculata* BM(NH) 76.4.8.2 Wellington			DM 1083 Holotype
Ear	6	18·5–19·1 (18·7)	10	18·2–18·7 (18·4)	14	17·4–18·9 (18·1)	—	—	17·5	8	17·7–18·6 (18·3)	18·1
Forearm	6	40·5–41·2 (40·7)	10	42·6–45·4 (44·0)	15	40·8–43·4 (42·0)	41·9	41·8	42·5	8	45·3–47·5 (46·4)	47·0
Thumb (c.u.)	6	7·1–7·9 (7·5)	10	7·8–8·6 (8·2)	14	8·0–8·9 (8·4)	7·5	7·0	7·9	8	8·9–10·3 (9·9)	10·0
Tibia	6	14·5–15·2 (14·9)	10	15·5–16·6 (16·1)	14	14·9–15·9 (15·4)	16·0	15·1	15·5	8	18·2–19·1 (18·7)	18·2
Foot (c.u.)	6	11·6–12·0 (11·9)	10	11·5–12·8 (12·1)	14	11·8–12·9 (12·2)	12·6	11·7	11·9	8	14·1–15·1 (14·6)	14·1
II^{m}	6	37·0–38·8 (37·8)	10	39·0–43·1 (41·1)	14	37·3–39·8 (38·4)	37·5	38·2	37·9	8	42·2–44·3 (43·1)	42·2
III^{m}	6	38·9–40·5 (39·7)	10	41·4–45·1 (43·3)	14	39·6–42·3 (41·2)	40·8	41·3	42·3	8	44·0–47·2 (45·7)	46·6
III^{1}	6	10·7–11·6 (11·1)	10	11·4–12·3 (11·8)	14	10·4–12·0 (11·6)	11·5	11·7	12·0	8	11·4–12·9 (12·4)	12·9
III^{2}	6	12·7–13·8 (13·2)	10	13·9–14·6 (14·2)	14	13·1–14·4 (13·7)	13·5	13·1	14·0	8	15·2–15·8 (15·4)	15·6
III^{3}	6	9·3–10·6 (10·1)	10	9·9–12·6 (11·6)	14	10·0–12·5 (11·3)	11·2	12·2	—	8	12·0–14·5 (13·2)	12·5
IV^{m}	6	38·0–39·8 (38·7)	10	41·1–44·2 (42·4)	14	38·7–41·9 (40·4)	39·8	40·0	41·1	8	42·8–45·3 (44·2)	44·8
IV^{1}	6	9·8–10·3 (10·1)	10	10·2–11·2 (10·8)	14	9·6–10·9 (10·4)	9·7	10·1	10·9	8	10·9–11·7 (11·3)	11·7
IV^{2}	6	12·4–13·3 (12·7)	10	12·7–14·0 (13·4)	14	12·1–13·4 (13·0)	13·5	12·9	13·6	8	14·6–15·1 (14·9)	14·5
V^{m}	6	35·1–36·0 (35·4)	10	36·5–40·0 (38·7)	14	35·4–38·2 (36·8)	37·2	36·4	37·8	8	39·3–42·2 (41·1)	42·2
V^{1}	6	6·1–6·7 (6·4)	10	6·6–7·2 (6·9)	14	6·0–6·8 (6·5)	6·4	6·4	7·0	8	6·4–7·8 (7·2)	7·4
V^{2}	6	10·4–11·0 (10·7)	10	11·0–11·6 (11·3)	14	9·6–11·3 (10·7)	10·7	11·1	11·6	8	11·4–12·1 (11·7)	11·7
V^{3}	6	6·5–7·2 (6·8)	10	6·4–9·1 (8·1)	14	6·0–8·5 (7·6)	—	—	8·0	8	8·0–8·6 (8·3)	8·3

Table 2 Cranial measurements of *Mystacina tuberculata* and *M. robusta*.

		M. tuberculata								*M. robusta*	
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'			DM 1083 Holotype
Greatest length of skull	5	18·7–19·5 (19·0)	6	19·2–19·8 (19·5)	10	18·9–20·0 (19·4)	19·3	19·3	5	22·2–23·5 (23·2)	23·4
Condylobasal length	5	17·3–18·0 (17·9)	5	18·3–19·1 (18·8)	9	17·9–18·9 (18·3)	18·1	18·0	5	21·0–22·5 (22·0)	22·5
Condylocanine length	5	16·7–17·7 (17·3)	5	17·7–18·4 (18·1)	9	17·4–18·2 (17·7)	17·4	17·4	5	20·3–21·6 (21·2)	21·4
Basal length	5	15·3–16·2 (15·7)	5	16·1–16·9 (16·4)	8	16·1–17·0 (16·4)	16·0	16·1	5	19·0–20·1 (19·7)	20·0
Basilar length	5	14·6–15·5 (15·0)	5	15·4–16·2 (15·7)	8	15·3–16·4 (15·7)	15·4	15·6	5	18·4–19·6 (19·1)	19·4
Palatal length	5	8·4–8·9 (8·6)	6	8·6–9·3 (8·9)	10	8·5–9·4 (8·8)	8·5	9·0	5	10·4–11·1 (10·8)	11·1
Palatilar length	5	7·7–8·2 (7·9)	6	7·9–8·6 (8·2)	10	7·7–8·6 (8·2)	7·7	8·3	5	9·8–10·5 (10·2)	10·4
Length palation—basion	5	6·9–7·3 (7·1)	5	7·3–7·8 (7·5)	8	7·3–8·0 (7·6)	7·7	7·3	5	8·6–9·2 (8·9)	9·0
Width across anteorbital foramina	5	4·8–5·2 (5·0)	6	5·0–5·6 (5·3)	10	5·0–5·3 (5·1)	5·1	4·8	5	5·3–5·7 (5·5)	5·7
Least interorbital width	5	5·1–5·5 (5·2)	6	5·4–5·7 (5·5)	10	5·3–5·9 (5·6)	5·4	5·7	5	6·3–6·8 (6·6)	6·6
Zygomatic width	5	10·2–10·8 (10·4)	2	11·0, 11·1	8	10·6–11·4 (11·0)	—	—	5	11·8–12·7 (12·3)	12·7
Width of braincase	5	8·6–9·2 (9·0)	6	9·0–9·4 (9·2)	10	8·8–9·7 (9·2)	8·9	9·4	3	10·5–10·9 (10·7)	10·5
Mastoid width	4	9·7–10·2 (10·0)	6	9·8–10·6 (10·2)	9	9·6–10·7 (10·1)	10·3	10·3	3	11·3–12·0 (11·7)	12·0
c^1–c^1 (crowns)	5	4·0–4·2 (4·1)	6	4·2–4·4 (4·3)	10	4·2–4·5 (4·3)	4·1	4·1	5	4·6–4·9 (4·7)	4·9
c^1–c^1 (alveoli)	5	3·9–4·1 (4·0)	6	4·0–4·3 (4·2)	10	4·1–4·4 (4·2)	4·0	3·9	5	4·4–4·7 (4·5)	4·7
m^3–m^3 (crowns)	5	6·8–7·1 (6·9)	6	7·2–7·3 (7·3)	10	7·2–7·8 (7·4)	7·1	7·3	5	8·0–8·3 (8·2)	8·3
m^3–m^3 (alveoli)	5	6·7–7·0 (6·8)	6	7·1–7·3 (7·2)	10	7·0–7·7 (7·3)	7·0	7·2	5	7·9–8·1 (8·0)	8·1
i–m^3	5	8·2–8·7 (8·4)	6	8·4–9·0 (8·7)	10	8·5–8·9 (8·7)	8·6	8·6	5	10·1–10·7 (10·4)	10·7
c–m^3	5	7·3–7·6 (7·4)	6	7·5–8·0 (7·7)	10	7·5–7·8 (7·7)	7·4	7·5	5	8·9–9·4 (9·2)	9·4
Length complete mandible from condyle	5	12·2–12·6 (12·3)	5	12·6–13·2 (12·8)	10	12·5–13·1 (12·8)	12·7	12·9	5	14·7–15·5 (15·3)	15·4
Length right ramus from condyle	5	12·4–12·9 (12·6)	6	12·8–13·6 (13·3)	10	12·9–13·7 (13·2)	13·2	13·3	5	15·4–16·0 (15·9)	15·9
c–m_3	5	7·7–7·9 (7·8)	6	8·0–8·5 (8·2)	10	7·8–8·4 (8·1)	8·1	8·2	5	9·6–10·0 (9·9)	10·0

DIAGNOSIS. A small, comparatively delicately proportioned species, as Dwyer (1962*a*) pointed out. The species is characterized externally by its relatively large ears which in length exceed 95% of the condylobasal length of the skull and by its prominent and narrow nostrils. *Mystacina tuberculata* is generally smaller than *M. robusta* (Tables 1 & 2) but apart from this there appear to be few other clear morphological features that separate the two species. The rostrum of *M. tuberculata* is not especially heavy or massive—Dwyer (1970) remarked that the smaller skulls that he had examined were proportionately broader and deeper than one larger example with weaker sagittal and occipital crests, the cranium rising more steeply from the facial region of the skull. In series there appears to be little difference in the proportions of the skull in the two species and no consistent difference in the cranial profile. As might be expected, the cranial crests of the smaller *M. tuberculata* are weaker. The difference in skull size between the two species (Table 2, Figs 1–7), however, is strongly marked and it is immediately apparent to which species any particular skull belongs.

REMARKS. Dwyer (1970) tabulates measurements of specimens (many subfossil) from various localities throughout New Zealand. His measurement 'maxillary row' is i–m^3 rather than c–m^3: in 20 examples of *M. tuberculata* measured in the course of the present study i-m^3 ranges from 8·2 to 9·0, c–m^3 from 7·3 to 8·0, and in 5 of *M. robusta* i–m^3 varies from 10·1 to 10·7, c–m^3 from 8·9 to 9·4. The skull lengths given by Dwyer correspond closely with those of skulls examined in London, as do his mandibular row measurements (the recessed lower incisors playing little part in this length which equals approximately c–m_3) and his maxillary row measurements agree closely with i–m^3 in these specimens. It seems therefore that he had included the upper incisor in this measurement.

Wear on the upper incisors of *Mystacina* has been investigated by Dwyer (1962*b*), who found that the erosion of these teeth correlated approximately with total skull length in two parallel series, one of smaller skulls which he thought were probably *M. t. tuberculata,* the other of larger skulls, which he thought were probably *M. t. robusta.* Although none of the skulls examined in this study shows the extreme erosion figured by this author for *M. tuberculata,* in general the series supports this view. In those of *M. tuberculata* the smallest from each locality have usually but not always the least worn incisors, and the largest specimens have incisors that show at least some degree of wear. A similar relationship prevails among the small series of *M. robusta* that has been examined. It is significant that a comparison of the smallest specimen (AIM M307) of *M. tuberculata* with a condylobasal length of 17·3, and one of the smaller (DM 1554) of *M. robusta* with a condylobasal length of 22·1, shows each to have incisors at a similar stage of wear. Those of DM 1554 are, however, larger and much more massive, as are all of the teeth of *M. robusta* when compared with those of *M. tuberculata.*

INTRASPECIFIC VARIATION. The specimens of *M. tuberculata* examined include examples from three populations: one from Omahuta at the extreme north of the North Island, another chiefly from Waimarino on the high volcanic plateau in the centre of the North Island, and the third from Codfish and Solomon Islands, off the southern coast of the South Island. Small but distinct differences between these groups can be distinguished and although the available material is limited these seem sufficient to justify formal recognition.

Mystacina tuberculata aupourica subsp. nov.

HOLOTYPE. ♀ AIM M309. Omahuta Kauri Sanctuary, Northland, North Island, New Zealand, 35°10'S, 175°37'E. This locality and the origins and history of the colony whence the holotype and other specimens came is documented in detail by Holloway (1976) and by Daniel (1976). Collected 22 May 1975 by M. J. Daniel. In alcohol, skull extracted.

OTHER MATERIAL. ♂♂ AIM M310–312. ♀♀ AIM M307–308 all from type locality (in alcohol, skulls of M307, M310–312 extracted).

DIAGNOSIS. Externally and cranially small (Tables 1 & 2) for the species; ears absolutely and relatively long (Tables 3 & 4); forearm and metacarpals short (Table 3); skull small, short and narrow (Table 2).

Table 3 Major external measurements of *Mystacina tuberculata* and *M. robusta* as a percentage of the condylobasal length.

	M. tuberculata									*M. robusta*	
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'			
Ear	5	103·3–106·9	5	96·3–101·1	9	94·7–101·6	—	—	4	80·4–88·1	
Forearm	5	218·6–234·1	5	232·8–237·7	9	224·0–235·4	232·6	233·3	4	207·2–215·7	
Thumb (c.u.)	5	41·0–43·3	5	41·4–44·4	9	42·3–49·7	41·4	38·8	4	41·7–49·0	
Tibia	5	80·9–84·9	5	85·1–88·0	9	81·4–86·9	88·4	83·8	4	80·9–85·7	
Foot	5	64·4–69·4	5	60·8–68·4	9	61·9–70·7	69·6	65·0	4	62·7–69·0	
II^{m}	5	203·8–218·0	5	213·1–230·5	9	201·1–216·3	207·2	212·2	4	186·7–200·9	
III^{m}	5	215·8–227·5	5	226·2–236·1	9	216·4–229·8	225·4	229·4	4	207·1–209·5	
IV^{m}	5	211·5–223·6	5	224·6–231·4	9	211·5–227·7	219·9	222·2	4	199·1–204·1	
V^{m}	5	192·9–202·9	5	199·5–212·8	9	193·4–206·6	205·5	202·2	4	187·5–190·5	

MEASUREMENTS OF HOLOTYPE. Length of ear 18·8; forearm 40·5; thumb (c.u.) 7·5; tibia 15·2; foot (c.u.) 12·0; II^{m} 38·2; III^{m} 39·4; III^{1} 10·7; III^{2} 13·0; III^{3} 10·5; IV^{m} 38·5; IV^{1} 9·8; IV^{2} 12·4; V^{m} 35·1; V^{1} 6·4; V^{2} 10·9; V^{3} 6·8; greatest length of skull 19·0; condylobasal length 17·9; condylocanine length 17·3; basal length 15·6; basilar length 14·8; palatal length 8·5; palatilar length 7·7; length palation—basion 7·1; width across anteorbital foramina 5·2; least interorbital width 5·1; zygomatic width 10·3; width of braincase 8·9; mastoid width 9·9; c^{1}–c^{1} (crowns) 4·0, (alveoli) 3·9; m^{3}–m^{3} (crowns) 6·8, (alveoli) 6·7; i–m^{3} 8·3; c–m^{3} 7·4; length complete mandible from condyles 12·3; length right ramus from condyle 12·5; c–m$_{3}$ 7·8.

DISTRIBUTION. So far known only from the type locality but likely to be found in suitable sites in the lowland areas of northern North Island, New Zealand, such as Waipoua kauri forest and on Little Barrier Island.

ETYMOLOGY. The subspecific name has been derived from the Maori name Aupouri or Aupori for the nothernmost peninsula of New Zealand. This has also been used as a basis for the name of the northland faunal area of New Zealand by Knox (1980) who calls this the Aupourian faunal province.

Mystacina tuberculata rhyacobia subsp. nov.

HOLOTYPE. ♀ AIM M304. Te Rimu area, upper Waimarino River, Kaimanawa Forest Park, SE of Lake Taupo, central North Island, New Zealand, 39°02′S, 175°56′E, *c.* 700 ft. Found with others in a hollow rimu tree that had been taken to the nearby sawmill at Turangi. Obtained July 1963 by G. R. S. Gerrard. In alcohol, skull extracted.

OTHER MATERIAL. ♂♂ AIM M301–303, M306, ♀♀ AIM M300, M305 all from type locality (in alcohol, skulls of M300–302, M305 extracted); ♀ MJD unnumbered Waipakihi River, Kaimanawa Forest Park, central North Island, 39°15′S, 175°48′E (in alcohol, skull extracted); ♂ DM 1432 Ruapehu, Tongariro National Park, central North Island, 39°17′S, 175°34′E (in alcohol);—MJD unnumbered Wairata, Waioeka State Forest, west of Urewera National Park, central North Island, 38°00′S, 177°17′E (in alcohol).

DIAGNOSIS. Larger externally and cranially (Tables 1 & 2) than *M. t. aupourica*; externally the largest of the species; ears relatively short (Tables 3 & 4); forearm and metacarpals long (Table 3); skull relatively large with longer, broader palate than in the northern lowland subspecies (Table 2).

MEASUREMENTS OF HOLOTYPE. Length of ear 18·5; forearm 44·2; thumb (c.u.) 8·3; tibia 16·3; foot (c.u.) 12·8;

Table 4 Length of ear, tibia and foot of *Mystacina tuberculata* and *M. robusta* as a percentage of the length of the forearm.

	M. tuberculata										
		Omahuta (*M. t. aupourica*)		Waimarino, etc. (*M. t. rhyacobia*)		Codfish I., etc. (*M. t. tuberculata*)	*M. t. tuberculata* BM(NH) 44.10.29.7 'New Zealand'	*M. t. tuberculata* BM(NH) 7.1.1.623 'New Zealand'	*M. t. tuberculata* BM(NH) 76.4.8.2 Wellington		*M. robusta*
Ear	6	45·4–47·7 (46·1)	10	40·6–43·4 (41·9)	14	41·1–45·0 (42·9)	—	—	41·2	8	38·0–40·8 (39·3)
Tibia	6	35·8–37·5 (36·7)	10	35·8–37·7 (36·7)	14	35·0–38·8 (36·6)	38·2	36·1	36·4	8	38·7–41·7 (40·3)
Foot (c.u.)	6	28·3–30·0 (29·2)	10	25·7–28·9 (27·4)	14	27·4–30·9 (29·2)	30·1	28·0	28·0	8	30·0–33·0 (31·4)

II^m 43·1; III^m 44·1; III^1 12·1; III^2 14·6; III^3 12·0; IV^m 43·2; IV^1 11·2; IV^2 13·1; V^m 39·8; V^1 6·9; V^2 11·0; V^3 8·1; greatest length of skull 19·5; condylobasal length 18·7; condylocanine length 18·1; basal length 16·4; basilar length 15·7; palatal length 8·8; palatilar length 8·1; length palation—basion 7·8; width across antorbital foramina 5·2; least interorbital width 5·4; zygomatic width ---; width of braincase 9·0; mastoid width 10·2; c^1–c^1 (crowns) 4·3, (alveoli) 4·2; m^3–m^3 (crowns) 7·3, (alveoli) 7·2; i–m^3 8·6; c–m^3 7·7; length complete mandible from condyles 12·8; length right ramus from condyle 13·2; c–m_3 8·2.

DISTRIBUTION. So far known only from the localities listed above but likely to be found elsewhere on the volcanic plateau in central North Island and in forests adjacent to it.

ETYMOLOGY. The subspecific name derives from ρναξ, a stream of lava, and from βιοσ, manner of living, a reference to the area in which this bat has been found.

Mystacina tuberculata tuberculata Gray, 1843

Synonymy under species heading.

ORIGINAL MATERIAL. The original specimens seen by Gray are discussed above.

TYPE LOCALITY. 'New Zealand': see discussion above.

SPECIMENS EXAMINED. —yg. BM(NH) 42.2.8.50 New Zealand (skin, skull); —BM(NH) 44.10.29.7 New Zealand (skin, skull); —BM(NH) 44.10.29.16 New Zealand (part skeleton); —yg. BM(NH) 49.3.2.1 New Zealand (skin, skull); —BM(NH) 76.4.8.2 New Zealand (in alcohol); — ♂ BM(NH) 89.10.27.2–3 Islands round Stewart Island (in alcohol); —BM(NH) 7.1.1.623 New Zealand (skin, skull); ♀ DM 1629(1) Big South Cape Island (in alcohol); ♀♀ BM(NH) 62.2116–2117 Solomon Island (in alcohol, skulls extracted); ♂♂ AIM M320–321, ♀♀ AIM M317–319, M322 Codfish Island, 46°47′S, 167°38′E (in alcohol, skulls of M317–318, M320–322 extracted).

DIAGNOSIS. Slightly larger externally than *M. t. aupourica* but with relatively shorter ears, longer thumbs and larger skull (Tables 1–4); ears and skull similar in proportions and size to those of *M. t. rhyacobia* but forearm and metacarpals short, their relative length much as in *M. t. aupourica* (Tables 1–3); palate long and broad (Table 2).

DISTRIBUTION. Extreme south of North Island, probably including forests of Tararua Range; possibly lowlands of South Island; islands off Stewart Island (last seen 1967 on Big South Cape and Solomon Islands, still present on Codfish Island); old record from Jacky Lee Island (Stead, 1936).

REMARKS. Examination of the measurements given by Dwyer (1970) shows that the smaller specimens that he reports from Karumu and Self Respect (38·5°S), Hukanui and Dartmoor Limestone (39·5°S) and Levin and Gouland Downs (41·0°S) are referable to *Mystacina tuberculata*. Other larger specimens from Puketiti (38·5°S), Hukunui and Bushface No. 1 (39·5°S), Gouland Downs (41·0°S), Pyramid Valley, Whitcombe Mts and Goulds (43–44°S) and Stewart Island (47·0°S) clearly represent *M. robusta*. Dwyer points out himself that two size groups are represented for the first three of these latitudes. It is interesting that the smallest specimens of *M. tuberculata* examined by Dwyer are from Karamu and Self Respect Caves, the most northerly localities from which his material came. These specimens correspond closely in size with the Omahuta population (*M. t. aupourica*), the most northerly and the smallest of those examined in London. On the other hand, one from 41·0°S (Levin and Gouland Downs) corresponds more closely in size to the Turangi population (*M. t. rhyacobia*) or to the nominate subspecies. Thus although Dwyer interpreted his measurements as displaying a continuous graduation from small to large, in fact they agree with the concept of a composite of two species, with the smaller of these dividing cranially into the two size groups into which the specimens forming the basis of the present study also fall.

Mystacina robusta Dwyer, 1962

Mystacina tuberculata robusta Dwyer, 1962*a*: 3, figs A, B, D. Big South Cape Island, New Zealand.

HOLOTYPE. ♂ DM 1083. Pukeotakeo, Big South Cape Island, New Zealand. Collected 29 April 1955 by L. C. Bell. In alcohol, skull extracted.

Specimens examined. ♂♂ DM 1083 (the holotype), 1553, ♀♀ DM 1555$^{(1)}$, 1555$^{(2)}$, 1629$^{(2)}$, 1629$^{(3)}$ 1629$^{(4)}$ Big South Cape Island; ♂DM 1554 Solomon Island, just north of Big South Cape Island (all in alcohol, skulls of DM 1083, 1553, 1554, 1629$^{(3)}$ extracted); ♀ OM unnumbered Solomon Island (skull and part skeleton).

Diagnosis. A large, robust bat with relatively shorter ears (Table 3) than *Mystacina tuberculata,* wide nostrils which lie rather closer to the muzzle than in that species, relatively slightly shorter forearm and wing elements (Table 3); rostrum slightly heavier and more massive than in *M. tuberculata,* the braincase generally rising a little less abruptly from the rostrum.

Measurements of holotype. See Tables 1 & 2.

Distribution. Big South Cape Island; Solomon Island; may occur in extreme south of South Island. It is possible that *Mystacina robusta* is now extinct, a recent survey by one of us (MJD) having found no recent evidence of its presence in the roost on Big South Cape: moreover, Maori bird hunters have not reported bats either from Big South Cape or from Solomon Island since 1967. The last positive record of *M. robusta* dates from 1965. Also, it seems likely that neither *M. robusta* nor *M. tuberculata* has ever been collected on Stewart Island although both may well have once occurred there, records from this island being based on specimens that came in fact from one or other of the surrounding islets such as Big South Cape or Solomon.

Remarks. The relatively shorter ears and wing elements of *Mystacina robusta* were interpreted by Dwyer (1962*a*) as evidence that *Mystacina* complied with Bergmann's and Allen's rules. The discovery of sub-fossil material evidently of the larger form in more northerly localities led Dwyer (1970) to re-examine the point. Having in this later paper concluded that *tuberculata* and *robusta* could be separated neither specifically or subspecifically, he had perforce to accept a wide range of size variation in *M. tuberculata* as he then understood it. His sample did not include small specimens from any southern locality, so he postulated that either only individuals with small extremities (i.e. cold-adapted) occurred in the south, the northern populations displaying the full range of size variation, or that alternatively the small individuals have only relatively recently replaced large individuals in the north. However, while it is true that a larger form with relatively shorter extremities (*M. robusta*) was found until 1965 only in the extreme south of New Zealand, it is clear from the material now available that it occurred there sympatrically with the smaller *M. tuberculata,* which also occurs in suitable locations over New Zealand as a whole—formerly the larger form seems to have been equally widespread.

Daniel (1979) has suggested that the dichotomy of the *Mystacina* stock probably occurred at a period when north–south isolation was pronounced and when the rapid onset of colder conditions, more extreme in the south, resulted in the two isolated populations evolving morphologically in accordance with the rules of Bergmann and Allen. He considered further that the most likely time for this to occur was the Pliocene and the beginning of the first Pleistocene glaciation. The smaller, less cold-tolerant form might well have survived subsequent glacial peaks in the kauri, podocarp and *Nothofagus* forests of northern New Zealand. The larger, better cold-adapted form could then have been predominant, perhaps surviving in forest refugia in the South Island. During warmer interglacials the two bats may have moved northward and southward with the re-establishment of forested areas. In more recent warmer times the smaller species has become established throughout New Zealand, and the larger form was found until 1965 only on two islands southwest of Stewart Island, although until recently both occurred in several parts of both North and South Islands. The reasons for the disappearance of the larger species are discussed by Daniel & Williams (1984).

Specimens examined in the course of this study tend to support this view. Those of *M. tuberculata* range from almost the northernmost extremity of New Zealand almost to the southernmost of the associated small islands. Thosee from the most northerly location are the smallest but have the largest ears, others from the volcanic plateau of North Island are the largest, but have relatively smaller ears and longer wing elements. Those from the southernmost population are externally slightly larger than the most northerly specimens but have smaller ears and are cranially larger, like the montane specimens from the North Island. Thus it is clear that some variation has occurred in this species, although its extent is small, and perhaps indicates a relatively recent post-glacial colonisation of much of the complex of islands. On the other hand, the greater differences separating *M. tuberculata* and *M. robusta* support a much earlier dichotomy as suggested by Daniel.

Acknowledgements

Our thanks are due to Dr Brian Gill of the Auckland Institute and Museum, to Dr G. R. F. Hicks of the National Museum, Wellington, and to the authorities of the Otago Museum, Dunedin for the loan of specimens essential to this study. We are indebted also to Drs B. A. Holloway and G. Kuschel of the Entomology Division, Department of Scientific Research, Auckland for their advice on the choice and etymology of the new names that we propose, and to Mr R. V. Melville of the International Commission on Zoological Nomenclature for his help in nomenclatorial matters.

Bibliography

Boie, F. 1822. Ueber Classification, Insonderheit der europaischen Vogel. *Isis,* Jena **10:** 545–564.

Daniel, M. J. 1976. Feeding by the short-tailed bat (*Mystacina tuberculata*) on fruit and possibly nectar. *New Zealand Journal of Zoology,* Wellington **3:** 391–398, 3 figs, 3 tabs.

—— 1979. The New Zealand short-tailed bat, *Mystacina tuberculata*; a review of present knowledge. *New Zealand Journal of Zoology,* Wellington **6:** 357–370, 5 figs, 3 tabs.

—— **& Williams, G. R.** (1984). A survey of the distribution, seasonal activity and roost sites of New Zealand bats. *New Zealand Journal of Ecology,* Wellington **7:** 9–25, 11 figs, 2 tabs.

Dobson, G. E. 1876. On *Mystacina tuberculata. Proceedings of the Zoological Society of London* 486–488, 1 fig.

—— 1878. *Catalogue of the Chiroptera in the collection of the British Museum.* Trustees of British Museum, London.

Dwyer, P. D. 1962*a*. Studies on the two New Zealand bats. *Zoology Publications from Victoria University of Wellington* No. 28: 1–28, 14 figs, 4 tabs, 4 maps.

—— 1962*b*. Wear to the incisors of the New Zealand short-tailed bat. *Records of the Dominion Museum,* Wellington **4:** 77–78, 12 figs.

—— 1970. Size variation in the New Zealand short-tailed bat. *Transactions of the Royal Society of New Zealand,* Wellington **12:** 239–243, 2 tabs.

Forster, J. R. 1844. In Lichtenstein, M. H. C. *Descriptiones Animalium quae in itinere ad Maris Australes Terras per annos 1772–74 suscepto collegit observatit et delinearit J. R. Forster . . . nunc demum editae auctoritatae . . . Academiae . . . curante H. Lichtenstein.* Koeniglich-Preussische Akademie, etc., Berlin.

Gray, J. E. 1843*a*. In Dieffenbach, E. *Travels in New Zealand; with contributions to the geography, geology, botany and natural history of that country.* John Murray, London. In two volumes.

—— 1843*b*. *List of the specimens of Mammalia in the collections of the British Museum.* Trustees of British Museum, London.

—— 1844. *Mammalia. In* Hinds, R. B. (Ed.). *The Zoology of the Voyage of H.M.S. Sulphur under the command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S., etc. during the years 1836–42.* Smith, Elder & Co., London.

—— 1875. *In* Richardson, J. & Gray, J. E. (Eds). *The Zoology of the Voyage of H.M.S. Erebus & Terror under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843.* 1. *Mammalia, Birds.* II. *Miscellanea.* E. W. Janson, London.

Holloway, B. A. 1976. A new bat-fly family from New Zealand (Diptera: Mystacinobiidae). *New Zealand Journal of Zoology,* Wellington **3:** 279–301, 68 figs, 2 tabs.

Honacki, J. H., Kinman, K. E. & Koeppl, J. W. 1982. *Mammal species of the world. A taxonomic and geographic reference.* Allen Press/ Association of Systematics Collections, Lawrence, Kansas.

Hutton, F. W. 1871. On the bats of New Zealand. *Transactions and Proceedings of the New Zealand Institute,* Wellington **4:** 184–186.

Knox, F. J. 1871. Observations on the New Zealand bats. *Transactions and Proceedings of the New Zealand Institute,* Wellington **4:** 186–188.

Knox, G. A. 1980. Plate tectonics and the evolution of intertidal and shallow-water benthic biotic distribution patterns of the SW Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology,* Amsterdam **31:** 267–297, 11 figs.

Lydekker, R. 1891. *In* Flower, W. H. & Lydekker, R. *An introduction to the study of mammals living and extinct*. A. & C. Black, London.

Neave, S. A. 1940. *Nomenclator Zoologicus. A list of the names of genera and subgenera in zoology from the tenth edition of Linnaeus 1758 to the end of 1935*. **3.** Zoological Society of London.

Sherborn, C. D. 1922. *Index Animalium sive index nominum quae als A.D. MDCCLVIII generibus et speciebus animalium imposita sunt*. Trustees of British Museum, London.

Stead, E. F. 1936. Notes on the short-tailed bat (*Mystacops tuberculatus*). *Transactions of the Royal Society of New Zealand*, Dunedin **66:** 188–191.

Thomas, O. 1905. On some Australasian mammals. *Annals and Magazine of Natural History: including Zoology, Botany and Geology*, London (7), **16:** 422–428.

Tomes, R. F. 1857. On two species of bats inhabiting New Zealand. *Proceedings of the Zoological Society of London* 134–142, 2 pls.

Manuscript accepted for publication 14 December 1984

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